FATAL ATTRACTION FOR AN IMPERILED SONGBIRD: IS CROPLAND IN THE NORTHERN GREAT PLAINS AN ECOLOGICAL TRAP FOR BREEDING THICK-BILLED LONGSPUR?

by

Amber Elizabeth Swicegood

A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Animal and Range Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

July 2022

ACKNOWLEDGEMENTS

This research was funded by the National Fish and Wildlife Foundation, the U.S. Fish and Wildlife Service's Migratory Bird Program, the Prairie Pothole Joint Venture, and the World Wildlife Fund. In particular, I would like to thank John Carlson, Mike Borgreen, Heather Nenninger, Macy Dugan, and Kathleen Tribby. I also want to thank Lee Sutcliffe and Aaron Yapper who were willing to share their expertise and volunteer numerous hours of nest searching efforts. I am very grateful to Sue Sather and Jeff Sather who allowed us to use their fieldhouse and provided a place for us to store equipment. I would also like to thank the private landowners who allowed access to their land for data collection. I also need to thank my committee. First of all, Lance McNew for his mentorship and continual support in every aspect of this project. Scott Somershoe for his work to secure the funding for this project, his consultation in its design and execution, and for visiting the field site. Marisa Sather for her help throughout the project from conception to completion, and for sharing her expertise of the study species, the Hi-Line, and for introducing me to many of the people who would make this project possible. Kevin Ellison for his guidance, support, and efforts in the field, and Jay Rotella for his mentorship and statistical guidance. Lastly, I need to thank the research technicians whose hard work and dedication made this project possible: Alicia Bachman, Justin Speicher, David DuBois, Megan Owens, Hillman Kraus, Janelle Bean, Evan Ward, and Evan Kuhel.

TABLE OF CONTENTS

LIST OF TABLES

Table Page

LIST OF TABLES CONTINUED

Table Page

LIST OF FIGURES

LIST OF FIGURES CONTINUED

ABSTRACT

Thick-billed longspur (*Rhynchophanes mccownii*) populations have declined 4% annually during the past 50 years. This species nests in recently disturbed or sparsely vegetated patches within native mixed-grass prairie and is also known to occur in crop fields in northeastern Montana during the breeding season. Maladaptive habitat selection may result in crop fields operating as ecological traps, but information on thick-billed longspur use of and demography in crop fields are lacking. We hypothesized that crop fields provide cues for territory selection, but frequent human disturbance and increased exposure to weather and predators should result in reduced reproductive success relative to native grassland habitats. To address this hypothesis, we 1) used dynamic occupancy models to compare arrival times of territorial male longspurs using data collected with autonomous acoustic recorders, 2) used open population distance sampling models to compare trends in longspur abundance over the breeding season, 3) compared indices of nest density and number of young fledged, and 4) used nest survival models to compare survival rates of nests between crop and native sites. Arrival times were similar in both site types and occupancy ranged from 0.52 ± 0.17SE on April 7 to 0.99 ± 0.01 on April 30. Bird abundances appeared to be mediated by vegetation biomass and drought conditions. Standardized nest densities were 0.15 ± 0.22SD and 0.23 ± 0.32 nests/hour/plot in crop and native sites, respectively; the number of young fledged per successful nest was similar in crop and native sites and averaged 2.9 ± 0.18SE. Nest survival was similar in crop and native sites and averaged 0.24 ± 0.03 SE (n=222 nests). The data did not support our ecological trap hypothesis: longspurs did not exhibit a clear preference for crop sites and reproductive output was not significantly reduced. Our results suggest that crop fields may expand nesting opportunities for thick-billed longspur in a region where native habitat may be limited.

CHAPTER ONE

LITERATURE REVIEW

Grassland birds have experienced steeper long-term declines than any other avian guild in North America during the past 50 years (Rosenberg et al. 2019, Sauer et al. 2020). Conservation of imperiled grassland birds is a management priority in northeastern Montana. This region contains some of the most extensive tracts of native prairie remaining in the United States and represents the core of the extant breeding range for several imperiled species (Cooper et al. 2001, Lenard et al. 2006). Four grassland birds of conservation concern exist in higher abundances here than elsewhere: Baird’s sparrow (*Ammodramus bairdii*), Sprague’s pipit (*Anthus spragueii*), chestnut-collared longspur (*Calcarius ornatus*), and thick-billed longspur (*Rhynchophanes mccownii*), and the region represents one of the last strongholds in the Northern Great Plains for these species (Samson and Knopf 1996, Cooper et al. 2001, Lenard et al. 2006). The thick-billed longspur is of particular conservation concern because it has unique habitat requirements that differentiate it from the other three species (Shaffer et al. 2019). Breeding Bird Surveys indicate thick-billed longspurs have declined 4% annually over the past 50 years (Fig 1; Sauer et al. 2020), but mechanisms driving declines are unknown.

The Northern Great Plains: Past and Present

More than 79% of grasslands in North America have been lost, primarily to land use conversion, 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, White 2000, Samson et al. 2004, Blann 2006, Ellis et al. 2010, Wright and Wimberly 2013). Indeed, intensification of agricultural practices is thought to be a leading driver of grassland bird population declines worldwide (Wilson et al. 2005, Quinn et al. 2017, Davis et al. 2020). Row-crop agriculture produces large monocultures devoid of much native plant and arthropod life and fails to support natural ecological connections and functions (White 2000). Landscape-scale monocultures are thought to be of little value to most wildlife species (Murphy 2003, Brennan and Kuvlesky Jr 2005). In addition, crop fields are disturbed frequently by farming activities including disking, seeding, and spraying, which are assumed to be detrimental to ground-nesting birds (Best 1986, Dale et al. 1997).

Remaining native grasslands have experienced large changes in ecosystem function and processes since Euro-American settlement. Grasslands of the Northern Great Plains evolved as dynamic systems, influenced by large-scale disturbance patterns. Drought, grazing, and fire interacted with local and regional temperature and moisture regimes to produce variable vegetative conditions at multiple spatial-temporal scales (Samson et al. 2004, Fuhlendorf et al. 2006). Keystone grazers including plains bison (*Bison bison bison*), black-tailed prairie dogs (*Cynomys ludovicianus*), and Rocky Mountain locusts (*Melanoplus spretus*; now extinct), altered plant communities and maintained heavily grazed areas (Lockwood and DeBrey 1990, Knapp et al. 1999, Fuhlendorf and Engle 2004, Augustine and Baker 2013). Drought was unpredictable and bison followed fire events, making use of the new growth and succulent forage. These patterns created feedback loops through fire and grazing that resulted in spatial and temporal variability of vegetation composition and structure across much of the Great Plains (Fuhlendorf and Engle 2001). Grassland birds evolved under such conditions, with the abundance of each species fluctuating locally as habitat conditions changed (Lenard et al. 2006). The dynamic nature of these disturbance patterns created a “shifting mosaic” of herbaceous structure and composition, which is key for maintaining biodiversity in prairie landscapes (Fuhlendorf et al. 2012).

Today, these large-scale disturbance forces are no longer prevalent in the Northern Great Plains (Knopf 1994, Fuhlendorf and Engle 2004, Samson et al. 2004). Most remaining grassland ecosystems are devoted to livestock grazing and rangeland management objectives are often geared toward maximizing sustainable livestock production by homogenizing utilization and therefore vegetation structure (Fuhlendorf et al. 2009). Management is often focused on removal of half the vegetative growth each year and uniform distribution of livestock to promote consistent utilization of forage (Toombs et al. 2010, Holechek 2011, Fuhlendorf et al. 2012). Rangeland health objectives include reducing the amount of bare ground, stabilizing soils, reducing potential for threshold change, and promoting desired plant communities (Briske et al. 2005, Fuhlendorf et al. 2012). Such “management for the middle” supports habitat conditions for a narrow suite of wildlife species (Samson and Knopf 1996, Samson et al. 2004, Fuhlendorf et al. 2012). Species that require habitat found at the extremes of the disturbance-succession gradient, including the thick-billed longspur, may not benefit from standard ‘take half, leave half’ management at landscape scales.

Thick-billed Longspur Conservation in the Northern Great Plains

Status and Distribution

The thick-billed longspur is considered a species of greatest conservation need (SGCN) in Montana and is of conservation concern in Arizona, Colorado, Kansas, New Mexico, North Dakota, Nebraska, Wyoming, Oklahoma, and Texas (Somershoe 2018). The current breeding range encompasses sections of mixed-grass and short-grass prairies of Montana, Wyoming, Colorado, Saskatchewan, and Alberta. Historically, the breeding range also included Oklahoma (no records since 1914; Nice 1931, Sutton 1967), western Minnesota (Currie 1890, Brown 1891; no records after 1900: Krause 1968, Green and Janssen 1975), and Manitoba (Taverner 1927). Two core breeding areas remain for the thick-billed longspur, one in northeastern Colorado and eastern Wyoming, and one in northeastern Montana and southern Alberta and Saskatchewan (Sauer et al. 2020). Wintering range includes the Chihuahuan Desert of northern Mexico, southern Arizona, eastern New Mexico, western Texas, and portions of Oklahoma (Somershoe 2018, Shaffer et al. 2019).

The grasslands of northern Valley County, Montana sustain one of the last strongholds for breeding thick-billed longspurs (Lenard et al. 2006, Somershoe 2018). The species has a strong preference for recently disturbed prairie, sparse vegetation, and bare ground, and is thought to use bare ground as a habitat selection cue upon arrival to the breeding grounds (Mickey 1943, Felske 1971, McLachlan 2007, Shaffer et al. 2019, With 2021). Thus, it is believed that the species was highly nomadic and followed large-scale disturbances (e.g., fire-grazing by bison, defoliation by locusts, expansive prairie dog towns), due to their adaptation to sparse vegetation cover and associated food resources during the breeding season (Knopf 1994, Fuhlendorf and Engle 2001, Lenard et al. 2006).

Nesting Ecology

Male thick-billed longspurs arrive on the breeding grounds in mid-April and most territories are established by late April or early May; females arrive in late April and the earliest nests are initiated the first week of May (DuBois 1937, Mickey 1943, Felske 1971, Greer 1988, With 2021). Thick-billed longspurs can be double-brooded with two peaks of nesting effort occurring in a single season (DuBois 1937, Greer 1988, Shaffer et al. 2019). The first peak nest initiation period occurs mid- to late May (Mickey 1943). The second peak occurs mid- to late June but is highly dependent on environmental conditions that year (Felske 1971, With 2021). Thick-billed longspurs will also renest after failure (Mickey 1943, Felske 1971). Territories are about one hectare in size and are often clumped within suitable, disturbed habitat patches (Mickey 1943, Felske 1971, Golding and Dreitz 2017). Thick-billed longspurs are thought to select breeding habitat along south-facing slopes and barren hillsides where snow melt occurs earliest and soil temperatures warm faster, providing better nesting conditions and an earlier invertebrate food supply (Felske 1971, Greer 1988, Shaffer et al. 2019).

Nests are built in shallow depressions in the ground. The open-cup nest is level with the ground and is made of dried woven grass and lined with finer material such as hair, feathers, or fine plant material. Clutch sizes are typically 3–4 eggs, incubation lasts 11–12 days, and fledging occurs 8–11 days after hatching (Mickey 1943, Felske 1971, Lenard et al. 2006, With 2021). Only females incubate eggs but both sexes of a breeding pair will brood nestlings after hatch and feed young. Nestling diet consists largely of grasshoppers (Orthoptera: Acrididae) and moths

(Lepidoptera), along with a variety of smaller insects and spiders (e.g., Diptera, Odonata, Araneae; Mickey 1943, Felske 1971). Adults continue to feed fledglings for three weeks after fledging, during which time the female may initiate a second brood (With 2021). Predation is the most common cause of nest failure (40–75%) with ground squirrels being a significant nest predator (Felske 1971, Greer and Anderson 1989, With 2021). Weather events sometimes cause nest failures; eggs and nestlings are subject to chilling if they become wet or cold (Mickey 1943, Felske 1971, With 2021).

The abundance and nesting effort of thick-billed longspurs fluctuate from year to year and depend heavily on environmental conditions. Regionally, longspurs may appear more abundant during dry years (Shaffer et al. 2019, With 2021). However, prolonged drought conditions and high temperatures will reduce the food supply causing cessation of nesting effort, and longspurs may also defer breeding during prolonged bouts of stormy weather or heavy rain (Shaffer et al. 2019).

Non-nesting Ecology

Little is known about thick-billed longspur fledgling survival, juvenile survival, or migration ecology (With 2021). During the non-breeding season, the species inhabits sparsely vegetated areas with high amounts of bare ground including plowed or fallow fields, heavily grazed pastures, and even dry lake beds in the southwestern U.S. and northern Mexico (Mickey 1943, Krause 1968, Smith et al. 2004, Muller and Ross 2022). Departure from the breeding grounds occurs between August and October, and birds arrive on wintering grounds in October or November (Saunders 1921, DuBois 1937, Phillips et al. 1964, Howell and Webb 1995).

Longspurs exhibit strong flocking behavior during migration and winter (Krause 1968) and diet consists primarily of grass and weed seeds (Grzybowski 1982, With 2021).

Current Conservation Concerns in Montana

Montana rangelands are not managed specifically for thick-billed longspurs, likely because managers do not wish to promote overgrazing or lose valuable grazing forage, even during the short-term (Sliwinski et al. 2018). In addition, these four grassland bird species of concern (Sprague's pipit, Baird's sparrow, chestnut-collared longspur, and thick-billed longspur) are typically lumped for conservation purposes (Shaffer et al. 2019). Management goals and objectives are rarely species-specific and often ignore the unique habitat needs of the thick-billed longspur (Vickery et al. 2000, Peterjohn 2003, Shaffer et al. 2019). Even managing for landscape heterogeneity may not be enough for thick-billed longspurs unless specific action is taken to create and maintain patches of short-stature vegetation. Currently, thick-billed longspurs persist in naturally drier portions of eastern Montana where drought and soil type generate the conditions necessary for successful nesting (Lenard et al. 2006, Shaffer et al. 2019).

Another concern unique to thick-billed longspur conservation is the species' use of croplands during the nesting season. Thick-billed longspurs are known to occur in fields used for row-crop production in northeastern Montana (Shaffer et al. 2019, M. Sather, pers. comm.). Although empirical information on thick-billed longspur nesting ecology in crop landscapes is limited, some old accounts mention the species' ability to "withstand the depredations of cultivation" (Felske 1971). Previous studies assessing nesting productivity of other grassland birds in crop fields have demonstrated negative consequences on reproductive success (Rodenhouse and Best 1983, Best 1986, Dale et al. 1997). Martin and Forsyth (2003) suggested a mismatch between use and productivity of thick-billed longspurs relative to different agricultural tillage practices, but information on how thick-billed longspurs use crop fields as nesting habitat and how this may influence population demographics in the region is lacking.

Given that current rangeland management practices do not focus on providing thick-billed longspur habitat and historic disturbance regimes have been substantially reduced, thick-billed longspurs may be using croplands as breeding habitat. Row-crop agriculture is now an important disturbance factor that produces extensive bare ground at large scales during spring when thick-billed longspurs arrive on the breeding grounds. Thus, crop fields may operate as a surrogate for historical native habitat given their appearance early in the season. If thick-billed longspurs use bare ground as a habitat selection cue, extensive tracts of bare ground and sparse vegetation provided by row-crop agriculture may potentially indicate to arriving males that such areas will provide suitable nesting habitat throughout the breeding season. However, the selection of crop fields during spring territory establishment could contribute to population declines if reproductive success is depressed, which may indicate that crop fields serve as an ecological trap.

Understanding Thick-billed Longspur Use of Croplands: An Ecological Trap?

Metapopulation theory suggests that geographic distributions of species are often composed of “source” and “sink” subpopulations (Pulliam 1988). A source produces a surplus of individuals, contributing to the maintenance of sinks. Population sinks often occur in marginal habitat and may be used when source habitat is limited or in the instance of competitive exclusion (Van Horne 1983, Johnson 2007, Gilroy et al. 2011). A mosaic of source and sink habitats across a landscape can maintain overall population densities greater than what could be maintained within the source habitats alone (Pulliam 1988, Delibes et al. 2001, Gundersen et al. 2001). In contrast, an ecological trap occurs when there is a mismatch between habitat selection cues and habitat quality (Battin 2004; Fig 2). Ecological traps are most commonly identified where human activities produce novel environmental cues or alter habitat quality associated with specific cues (Robertson et al. 2013, Hale and Swearer 2016, Simon and Fortin 2019). The quality of source and sink habitats may vary over time, but ecological traps are always detrimental for a population. An ecological trap also differs from a population sink in that animals exhibit preferential selection of trap habitats (Schlaepfer et al. 2002, Battin 2004, Gilroy et al. 2011).

Ideal free distribution theory that underpins source-sink population models assumes that animals always exhibit optimal habitat selection when distributing themselves among habitat patches and that the fittest individuals obtain the highest quality territories (Battin 2004). In reality, individuals are most likely to select habitat according to evolutionarily predisposed cues. Ecological traps are attractive because they often contain preferred cues (Delibes et al. 2001, Abrams et al. 2012, Fletcher Jr et al. 2012, Hale et al. 2015, Hale and Swearer 2016). From a management perspective, increasing the amount of source habitat across the landscape in the presence of an ecological trap may provide minimal benefits if individuals still select for trap habitats (Battin 2004). Detecting the presence of an ecological trap involves demonstrating 1) species preference for trap habitat and 2) evidence of reduced fitness in trap habitats. Importantly, high population densities in trap habitats do not necessarily equate to preference for that habitat type (Van Horne 1983, Vickery et al. 1992). Territory density alone is not enough to assess habitat quality and infer the presence of a trap, but clarity may arise when this variable is used in conjunction with other variables. Settlement patterns of territorial males, nest success, and territory density or abundance estimates have successfully been used in combination to test for the presence of an ecological trap for breeding passerines (Remeš 2003, Lloyd and Martin 2005, Weldon and Haddad 2005, Robertson and Hutto 2006).

Crop fields have been found to be poor nesting habitat for many songbirds (Rodenhouse and Best 1983, Frawley and Best 1991, Dale et al. 1997) but may be beneficial to others, even expanding nesting opportunities in some systems (Martin and Forsyth 2003, Weintraub et al. 2016). Some studies have demonstrated evidence of crop fields operating as ecological traps for ground nesting birds, primarily because birds are attracted to crop fields as nesting habitat but nests are destroyed by mechanical farming operations (Basore et al. 1986, Best 1986). This may also be the case for birds using hayfields that are cut during the nesting season (Bollinger et al. 1990). More recently, changes in nest initiation in response to climate change interacting with timing of farming operations have generated phenological mismatches, creating new ecological traps in some types of cropping systems (Santangeli et al. 2018).

In northern Montana, crop fields are largely bare until mid-summer and soils are more exposed to wind, water erosion, and large temperature swings than are soils in native prairie sites. Cultivated soils are less stable than soils in native prairie and topsoil may be lost when it is exposed to wind and rain without native vegetation to provide stability (MacRae et al. 1990, Pimentel et al. 1995, Van Oost et al. 2005, Menendez III et al. 2020). The capacity for water retention is altered in cultivated cropland, increasing negative impacts resulting from water erosion and concentrated runoff after heavy rains (Van Pelt et al. 2017). Pesticides and fertilizers may drastically alter soil composition and reduce or eliminate arthropod communities (White

2000). Collectively, these processes may present hazards for ground nesting songbirds that include effects on thermoregulation, nest destruction resulting from heavy rains and other weather events, exposure to dangerous chemicals, and a reduction in food availability for adults and nestlings. In addition, crop fields are disturbed multiple times during the breeding season by farming activities such as plowing, disking, and spraying. Most crops grow rapidly into a dense monocultures, changing from short-stature vegetative conditions (residual crop stubble ~15–20 cm tall) with large amounts of bare ground to tall, dense vegetative conditions (closed-canopy crops ~60–70 cm tall) unsuitable for thick-billed longspurs (Wilson et al. 2005).

Reduced reproductive success of thick-billed longspurs in crop fields relative to native prairie would suggest either an ecological trap or a demographic sink. A demonstrated preference for crop fields, however, would lend support to the ecological trap hypothesis. Upon arrival to the breeding grounds in spring, vast expanses of bare ground provided by crop fields may imitate historically preferred breeding habitat. If thick-billed longspurs use bare ground as a habitat selection cue, it is plausible that they may preferentially select crop fields as nesting habitat. Changes in longspur territory densities and nest densities in crop fields compared with native sites can provide insight on changing habitat preferences and lost nesting opportunities as crop vegetation changes over the growing season.

Current management practices for grassland birds include restoration of crop fields back to native prairie through cultivation of native seed mixes. If crop fields operate as ecological traps for thick-billed longspur, current management practices may not be sufficient for mitigating population declines as the species may continue to use preferred crop habitat regardless of how much native habitat is available. However, if crop fields are benefitting thick-billed longspur by providing appropriate nesting habitat where otherwise limited, restoration of fallow crop fields may be detrimental to thick-billed longspur populations.

Herein I assess thick-billed longspur preference and use of crop fields, along with subsequent nest survival and reproductive output relative to native prairie habitats. To put potential effects of habitat strata into context, I evaluate differences in structural habitat conditions between crop and native sites and assess changes in vegetation conditions in crop sites over the breeding season. Finally, I tie all of these concepts together and provide management recommendations based on findings.

CHAPTER TWO

EVALUATING CROPLAND AS AN ECOLOGICAL TRAP FOR BREEDING THICK-BILLED LONGSPUR IN THE NORTHERN GREAT PLAINS

Introduction

The thick-billed longspur is a grassland songbird endemic to the short- and mixed-grass prairies of North America (Knopf 1996). Breeding Bird Surveys indicate thick-billed longspurs have declined 4% annually over the past 50 years (Sauer et al. 2020), but mechanisms driving declines are unknown. Habitat for thick-billed longspurs is patchy on native sites, limiting distributions at regional scales and making this a focal species for U.S. Fish and Wildlife Service (USFWS) conservation efforts (Somershoe 2018). As a group, grassland birds have experienced some of the steepest population declines of any avian guild in North America over the past 50 years (Knopf 1994, Sauer et al. 2020). While factors such as fire suppression, overgrazing, desertification, and the introduction of non-native plant species have contributed to degradation of North American grasslands, conversion to large-scale, row-crop agriculture remains one of the greatest threats to grassland systems (Knapp et al. 1999, White 2000, Samson et al. 2004, Blann 2006, Ellis et al. 2010, Wright and Wimberly 2013).

Thick-billed longspurs (hereafter “longspurs”) have a unique preference for recently disturbed or sparsely vegetated grassland habitats, and historically relied on large-scale natural disturbance regimes to maintain suitable habitat patches within native prairies (Mickey 1943, Felske 1971, McLachlan 2007, Shaffer et al. 2019, With 2021). Keystone grazers including plains bison (*Bison bison bison*), black-tailed prairie dogs (*Cynomys ludovicianus*), and Rocky

Mountain locusts (*Melanoplus spretus*; now extinct), altered plant communities and maintained heavily grazed areas (Lockwood and DeBrey 1990, Knapp et al. 1999, Fuhlendorf and Engle 2004, Augustine and Baker 2013). Drought, grazing, and fire interacted with local and regional temperature and moisture regimes to produce variable vegetative conditions at the landscape scale (Samson et al. 2004). However, these dynamic disturbance events that once shaped prairie ecosystems are no longer prevalent at large scales in the Northern Great Plains (Samson and Knopf 1996, Fuhlendorf and Engle 2004, Samson et al. 2004, Hovick et al. 2015).

Most remaining grassland ecosystems are devoted to livestock grazing and rangeland management objectives are oriented toward maximizing livestock production by homogenizing vegetation structure at landscape scales (Fuhlendorf et al. 2009). Objectives focus on consistent removal of half the vegetative growth each year and uniform distribution of livestock to promote homogenous utilization of forage (Toombs et al. 2010, Holechek 2011, Fuhlendorf et al. 2012). Rangeland health objectives include reducing the amount of bare ground, stabilizing soils, reducing potential for threshold change, and promoting desired plant communities (Briske et al. 2005, Fuhlendorf et al. 2012). Such “management for the middle” supports habitat conditions for a narrow suite of wildlife species (Samson and Knopf 1996, Samson et al. 2004, Fuhlendorf et al. 2012). Species that require habitat found at the extremes of the disturbance-succession gradient, including the thick-billed longspur, likely do not benefit from standard ‘take half, leave half’ management.

Longspurs are also known to occur in fields used for row-crop production within the core of their breeding distribution in northeastern Montana (Felske 1971, Shaffer et al. 2019). Given that current rangeland management practices do not focus on providing thick-billed longspur habitat and disturbance regimes have been altered, longspurs may be using croplands as breeding habitat. Row-crop agriculture is now an important disturbance factor that produces extensive bare ground at large scales during spring when longspurs arrive on the breeding grounds. Thus, crop fields may operate as a surrogate for historical native habitat given their appearance early in the season. If longspurs use bare ground as a habitat selection cue, extensive tracts of bare ground and sparse vegetation provided by row-crop agriculture may potentially indicate to arriving males that such areas will provide suitable nesting habitat throughout the breeding season. However, the selection of crop fields during spring territory establishment could contribute to population declines if reproductive success is depressed and may indicate crop fields serve as an ecological trap.

Wildlife populations are often composed of sources and sinks: a source population contributes to population growth, whereas sink populations often occur in marginal habitat and are supported by source populations (Pulliam 1988, Gilroy et al. 2011). An ecological trap differs from a population sink in that animals exhibit preferential selection of trap habitats (Schlaepfer et al. 2002, Battin 2004, Gilroy et al. 2011). Ecological traps occur when there is a mismatch between habitat selection cues and habitat quality and are most commonly identified where human activities produce novel environmental cues or alter habitat quality associated with a particular cue (Battin 2004, Robertson et al. 2013, Hale and Swearer 2016, Simon and Fortin 2019). Ideal free distribution theory that underpins source-sink population models assumes that animals always exhibit optimal habitat selection when distributing themselves among habitat patches and that the fittest individuals obtain the highest-quality territories (Battin 2004). In reality, individuals are most likely to select habitat according to evolutionarily predisposed cues, and ecological traps are attractive because they often contain these preferred cues (Delibes et al. 2001, Abrams et al. 2012, Fletcher Jr et al. 2012, Hale et al. 2015, Hale and Swearer 2016).

Detecting the presence of an ecological trap involves demonstrating 1) species 'preference' (i.e., earlier selection and higher use) for trap habitat and 2) evidence of reduced fitness in trap habitats. Importantly, high population densities in trap habitats do not necessarily equate to preference for that habitat type (Van Horne 1983, Vickery et al. 1992). Territory density or animal abundance is not enough to assess habitat quality and infer the presence of a trap, but clarity may arise when this information is used in conjunction with other variables. Settlement patterns of territorial males, nest success, and territory density/abundance estimates have successfully been used in combination to test for the presence of an ecological trap for breeding passerines (Remeš 2003, Lloyd and Martin 2005, Weldon and Haddad 2005, Robertson and Hutto 2006).

Reduced longspur reproductive success in crop fields relative to native prairie would suggest either an ecological trap or a demographic sink. A demonstrated preference for this habitat type would lend support to the ecological trap hypothesis. Upon arrival to the breeding grounds in spring, large expanses of bare ground provided by crop fields may imitate historically preferred breeding habitat. If longspurs use bare ground as a habitat selection cue, it is plausible that they may select crop fields as a surrogate for historic nesting habitat. Earlier and higher rates of settlement of crop fields would indicate some level of preference for crop fields; when coupled with lower reproductive success in crop fields, such findings would support the ecological trap hypothesis (Lloyd and Martin 2005, Robertson and Hutto 2006). Delayed settlement of crop fields until after native sites are occupied, coupled with lower reproductive success, would suggest a population sink (Gilroy and Sutherland 2007).

Our objectives were to: 1) evaluate settlement patterns of territorial male longspurs in crop and native sites upon arrival to the breeding grounds in spring, 2) compare bird abundance and nest densities between site types and assess changes in abundance over the breeding season, 3) compare differences in nest survival and reproductive output between crop and native sites, 4) quantify differences in vegetation structure between crop and native sites and compare changes in habitat structure over the breeding season, and 5) provide management recommendations for thick-billed longspur populations in northeastern Montana. If crop fields are ecological traps for longspurs, we expected to observe the following:

1. Earlier settlement of crop fields: If, at the regional level, longspurs prefer crop sites over native sites and use bare ground as a habitat selection cue, we expect territorial males to settle first in crop sites. By documenting arrival or flow of individuals into different habitats, we can attempt to assess longspur preference for crop sites relative to native sites (Battin 2004).
2. Higher abundance in crop fields: We expect to see higher longspur abundance in crop sites relative to native sites. While animal abundance cannot inform us of habitat preference or habitat quality (Van Horne 1983, Vickery et al. 1992), this information will inform us of the degree of use of crop fields by longspurs (Robertson and Hutto 2006).
3. Higher nest density in crop fields: If crop fields are attractive nesting habitat for thick-billed longspurs, we also predict that overall nest densities in crop sites will be higher than densities in native sites. Higher nest densities in crop sites would indicate higher use

of crop fields as nesting habitat, indicating that either a) nesting sites in native habitat are limited or b) longspurs prefer crop sites for nesting (Robertson and Hutto 2006).

4. Lower nest survival or reproductive output: We predict that nest survival and the number of chicks fledged per successful nest will be lower in crop sites compared to native sites. Soils in crop fields are more exposed to wind, water erosion, and large temperature swings than are soils in native sites (MacRae et al. 1990, Pimentel et al. 1995, Van Oost et al. 2005, Menendez III et al. 2020). Pesticides and fertilizers may drastically alter soil composition and reduce or eliminate arthropod communities (White 2000). These processes may present hazards for ground nesting songbirds that include effects on thermoregulation, nest destruction resulting from flash floods and other weather events, exposure to dangerous chemicals, and a reduction in food availability for adults and nestlings. In addition, crop fields are disturbed multiple times during the breeding season by farming activities such as plowing, disking, and spraying, and most crops grow into a dense monoculture by mid-late summer, creating unsuitable conditions for longspurs. Previous studies assessing nesting productivity of other grassland birds in crop fields have demonstrated negative consequences on reproductive success (Rodenhouse and Best 1983, Best 1986, Dale et al. 1997).

Methods

Study Area

The study area was located in northern Valley County, Montana (Fig 3). 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 from below 0° C in winter to 20–25° C in summer. 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 incorporates cultivated crop fields in the eastern portion and native mixed-grass prairie in the western portion. Federal lands and private ranches occur west of Opheim and Baylor, and the Bitter Creek Wilderness Study Area, characterized by its unspoiled badlands, sits 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 dominate and include western wheatgrass (*Pascopyrum smithii*), needle-and-thread (*Hesperostipa comata*), prairie junegrass (*Koeleria macrantha*), green needlegrass (*Nassella viridula),* and Sandberg bluegrass (*Poa secunda*) and threadleaf sedge (*Carex filifolia*). One warm season grass, blue grama (*Bouteloua gracilis*), is present in some sites. Spikemoss (*Selaginella densa*) can be locally abundant as well. Shrub cover is low-moderate across most of this region (Charboneau et al. 2013).

Northern Valley County is characterized by large expanses of drier areas unsuitable for cultivation and wetter areas used for row-crop production. Arid patches within large tracts of intact native mixed-grass prairie provide habitat for thick-billed longspur and the species is known to be locally abundant in such areas (Lenard et al. 2006, Lipsey 2015). These native sites consist of aridic, well-drained glacial soils of the Elloam series and have relatively low vegetation production potential (<1000 kg ha^{-1}). Crop fields are characterized by extensive amounts of bare ground, particularly in early spring. Primary crops in this region include spring wheat, barley, lentil, pea, flax, and canola. As the season progresses, the crop type dictates how rapidly these landscapes change and the degree to which plant biomass and vegetative cover increase. In some areas wheat farming is conducted on a 50:50 rotation with 50% of the acreage being left fallow each year to conserve soil moisture and nutrients (M. Sather, USFWS, pers. comm.). Pulse crops such as pea and lentil 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.).

Field Methods

Longspur Settlement

We deployed 24 autonomous acoustic recorders (Wildlife Acoustics model SM4, Maynard, MA; hereafter “song meters”) to assess arrival times and settlement patterns of territorial male thick-billed 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) accounts 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) deployed in crop fields and half deployed in native grassland sites. We selected sites that were no more than 25 kilometers 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. All song meters recorded in stereo at 32 kHz, a left and right gain of 16 dB, and left and right filter at 1,000 Hz. Upon removal from the field, a trained technician manually reviewed each 3-minute recording and documented whether a longspur was detected or not (detected = 1, not detected = 0). We marked any recordings ≥ 25% obscured by wind or other noise as "NA".

Longspur Abundance

Occurrence Surveys. – To locate areas used by thick-billed longspurs, we randomly generated 100, 64-ha sampling plots in both crop and native sites. We excluded survey areas that were >2 km from a road, had rangeland productivity ≥1,100 kg ha^{-1} (Lipsey and Naugle 2017), and where private land access was denied. 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 (Fig 4). 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 each transect was completed within 40 minutes. Observers were trained to avoid double-counting birds when turning transect corners. Surveys began one half hour before sunrise and stopped at 10:00 hours. We did not conduct surveys if wind speed was >25 km hr^{-1} or when it was raining. We recorded survey covariates including observer, percent cloud cover, temperature, wind speed, date, GPS starting point, and transect start/end times.

Abundance surveys. – Within plots identified as being occupied by longspurs, we generated 16-ha survey plots within which we monitored longspur populations for the remainder of the 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 plots from areas where thick-billed longspur occurred.

We used distance sampling methods to estimate the abundance of territorial male longspurs multiple times throughout the breeding season. We conducted 6 rounds of line transect surveys within 16-ha survey plots 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 (Fig 5). 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. Each transect was completed within 30 minutes and surveys began 15 minutes before sunrise and stopped at 9:00 hours.

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 capture reproductive effort throughout the entire nesting season (With 2021). We searched for nests from sunrise until 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 we used behavioral observations to find nests (Martin and Geupel 1993, Winter et al. 2003). Each observer moved to a new plot after 60 minutes if no female longspurs were observed. We observed longspurs from a distance of ≥30 m. We supplemented behavioral nest searching with standard rope dragging methods (Klett et al. 1986, Koford 1999). We began surveys at one randomly selected corner of the plot and systematically covered the entire plot with the rope.

Nest Monitoring. – Upon finding a nest, we recorded the geographical coordinates with a handheld GPS and marked the nest location with two 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 behavior of adults, 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 (Jonsomjit 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 bowl. We deemed a nest successful if adults were observed feeding fledglings proximal to the nest, fledglings were observed near the nest bowl, territorial adults were present with food or directed aggressive behaviors toward observers, or fecal material was present around the nest bowl and the nestlings reached the appropriate age to fledge. A nest was considered successful if ≥1 chick fledged (Ralph 1993, Jones et al. 2010).

Habitat Conditions

We evaluated habitat conditions (e.g., vegetation measures) at two spatial scales, the nest site and the survey plot. Vegetation measures were collected at every nest site 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 occurring in crop fields and native prairie sites, respectively. Vegetation conditions in crop fields were fairly homogenous and required fewer sampling points. We measured a suite of 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 coverages of grass, forbs, shrubs, litter, and bare ground within a 20 × 50 cm sampling frame at the sampling point and at 4 locations 0.5 m from the point in each cardinal direction (Daubenmire 1959). Coverages were recorded within six percentage classes (0%, 1–5%, 6–25%, 26–50%, 51–75%, 76–95%, and 96–100%). We listed all plant species, in order of decreasing abundance, found within a 2-meter radius of the point center. Lichen and spikemoss were abundant in native sites and were recorded in the plant inventory list as well as percent ground cover within each frame. 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 of the sampling point as the presence of shrubs has been known to influence nest density or detection of nests for many grassland passerines (Davis 2005, Pulliam et al. 2021).

Analytical Methods

Longspur Settlement

We used dynamic (multi-season) occupancy models to evaluate whether settlement patterns of longspurs differed between crop and native sites (MacKenzie et al. 2003). Dynamic 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) across time while accounting for spatially variable detection probability (MacKenzie et al. 2003, Mackenzie 2006). The design consists of k secondary survey periods within T primary periods and models rely on the following assumptions satisfied by our study design: 1) sites are closed to changes in true occurrence within primary sampling periods, 2) replicate surveys at each site within a primary period are independent, and 3) there are no false-positive detections (MacKenzie et al. 2003). 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 dynamic occupancy models using the ‘colext’ function in R package ‘unmarked’ (Fiske and Chandler 2011, Kéry 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).

Next, we developed a suite of models to evaluate the effects of survey conditions on detection probability. Variables hypothesized to influence detection probability 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 the 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 and identify a parsimonious sub-model for detection probability. Starting with a full model including all covariates, we eliminated the least important covariates sequentially based on the lowest absolute value of β/SE. If removal of a covariate resulted in lower $QAIC_c$, we removed the higher order model from the model set. When no covariates could be removed without increasing $QAIC_c$, we stopped the process (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, so when removal of a single covariate increased $QAIC_c$ by ≤2 units and the maximized quasi log-likelihood changed marginally, the additional covariate was considered uninformative and this higher order model was also eliminated (Devries et al. 2008, Arnold 2010, Burnham et al. 2011). After a parsimonious sub-model for detection was identified, it was retained in subsequent evaluations of occupancy and settlement.

Because some birds had already arrived at the study area prior to our deployment of song meters, 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).

Longspur Abundance

We used open-population distance sampling models to estimate longspur abundance in crop and native sites and assess whether abundance changed differentially during 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). Observations were recorded along with perpendicular distance from the transect line, and probability of detecting an individual was assumed to be a decreasing function of distance from the transect line with probability on the line being equal to 1. Other assumptions included a) animals were distributed uniformly in space relative to the transect, b) distance was recorded accurately, c) animals were recorded at their initial location and did not move during the survey or in response to the observer, and d) animals were not double-counted (Buckland et al. 2001). The distance sampling framework has been expanded to allow abundance to be modeled as a function of site-specific covariates, permitting ecological inference about spatial variation in abundance (Royle et al. 2004). Recently, this framework has been expanded even further to 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 to estimate the best-fitting detection function and mixture type based on our data. We used the ‘trend’ dynamics parameterization as we were only interested in modeling trends in longspur abundance over the season and were not interested in estimating explicit population dynamics. The hazard rate detection function was most supported by our data and the negative binomial was the best supported mixture type, indicating there was some degree of overdispersion in the 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'. 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). Even with the negative binomial distribution, we found evidence of moderate overdispersion ($\hat{c} = 1.9$). Because the negative binomial model may have trouble stabilizing estimates and is known to sometimes overestimate population abundance (Ver Hoef and Boveng 2007, Kery and Royle 2015), we ran diagnostic tests by systematically increasing the parameter K to assess whether the maximized log-likelihood stabilized. Although estimates did stabilize at high values of K (K = 150), abundance estimates from this model were much higher than we deemed biologically reasonable, so we used the Poisson distribution for all subsequent models, inflated estimated standard errors by $\sqrt{\hat{c}}$, and based 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).

Next, we developed a suite of 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 within the first 2–3 hours after sunrise (With 2021). Initial screening indicated that detection probability 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.

Next, we evaluated whether initial abundance and seasonal trends differed by habitat type (crop vs. native; Table 2). We developed a set of 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 empirical Bayes 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).

Nest Phenology, Survival, and Reproductive Output

Nest Phenology. – For each nest, we calculated initiation date as the day the last egg was laid, which is when incubation typically begins for passerines (Gill 1990, George et al. 1992). Initiation date was estimated based on laying sequence, hatch date, or chick age and assuming an incubation period of 12 d. 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 in these patterns 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 12 competing models that included all combinations of habitat type, initiation date, and year. We also included one model containing a quadratic effect of initiation date because other studies have shown DSR to be either 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 two additional models, one with a pseudo-threshold effect of initiation date and one including an interaction term with habitat type. This resulted in a candidate set of 15 models (Table 3). 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., DSR^{25} 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. However, 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; observers were rotated through different plots each day.

We tabulated maximum clutch size for all nests with known fates as well as the number of young fledged per successful nest. The number of young fledged was recorded as the number of chicks present during 8–10 d after hatching, 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 assess whether 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 using Akaike's Information Criterion corrected for finite sample size (AIC_c; Burnham et al. 2011) and used the best-fitting model to estimate the number of young fledged per successful nest.

Habitat Conditions

We used generalized linear models to test hypotheses that specific vegetation attributes differed significantly between crop and native sites, that longspur habitat changed structurally over the summer as plants grew, and that such changes in habitat attributes are more extreme in crop sites than in native sites. Vegetation variables included VOR, bare ground cover, grass and forb cover, litter cover and litter depth. For proportional response data (e.g., vegetation 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 vegetation variable, we built and evaluated the same set of competing models representing *a priori* hypothesized relationships between habitat type and survey round (Table 5).

We evaluated relative model support 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 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).

Results

Longspur Settlement

We deployed recorders at 8 sites in 2020 and 16 sites in 2021, half in crop fields and half in native sites. Recordings from two song meters located in native sites in 2020 and one song meter located in a crop field in 2021 were discarded because longspurs never established territories at those locations. Recordings from one song meter at a native site in 2021 were not retrievable due to equipment malfunction, resulting in useable data from 2 song meters at native sites and 4 song meters at crop sites in 2020, and 7 song meters at native sites and 7 song meters at crop sites in 2021. Overall, we collected >37 hours of useable recordings in 2020 and >100 hours in 2021. On 10 April 2020, 1 out of 4 crop sites were occupied and 0 out of 2 native sites were occupied. On 29 April 2020, all sites were occupied. On 7 April 2021, 4 out of 7 crop sites were occupied and 3 out of 7 native sites were occupied. On 30 April 2021, all sites were occupied. For occupied sites on the first survey day of the year, the number of recordings in which longspurs were detected ranged from 1–5 out of 6 recordings. On the final survey day, the number of recordings containing detections ranged from 5–6 out of 6 recordings.

Detection probability. – The top model for detection probability contained an effect of Julian day, minimum temperature, and a quadratic effect of minutes past sunrise (time) (QAIC$_c$ w_i = 0.97; Table 6). Detection probability increased with Julian day (β = 0.99 ± 0.13 SE) and increased in response to minimum temperature (β = 0.08 ± 0.02). Detection probability was maximized at ~90 – 100 minutes past sunrise, or 1.5 hours after sunrise (Fig 6).

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 6). We found no evidence that settlement probability differed by habitat type with the model containing an effect of Julian day carrying full support (QAIC$_c$ w_i = 0.98). Settlement probability increased for both habitat types with Julian day (β = 2.24 ± 0.68). Derived estimates of true occupancy for both crop and native sites increased from 0.52 (± 0.17 SE) on 7 April to 0.99 (± 0.01) on 30 April (Fig 7).

Longspur Abundance

In 2020, we conducted initial occurrence surveys in 80 plots (36 crop and 44 native); 67% of crop plots were occupied by thick-billed longspur and 20% of native plots were occupied. In 2021, we conducted initial surveys in 62 plots (35 crop and 27 native); 91% of crop plots were occupied 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. The mean ± SD number of male longspurs observed was of 5.4 ± 4.4 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 male longspurs per plot in crop and native sites, respectively. Most crop plots were spring wheat (28 plots); we surveyed 4 summer fallow plots in 2020 and 8 in 2021 (Table 7). We analyzed data separately for the two years because differences in weather and drought conditions were likely to produce different population trends.

Detection probability. – During both years, the top model for detection probability contained an effect of observer group (Table 8). 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 (Fig 8). 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 8). Expected initial abundance in crop sites was 17.4 ± 4.1SE 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. Estimated 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 (Fig 9).

In 2021, we found no evidence 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 8). 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 (λ = 1.03 ± 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; Fig 9).

Nest Phenology, Survival, and Reproductive Output

During 2020–21 we located 240 longspur nests, 111 in crop sites and 129 in native sites. Of these, 174 nests were located using behavioral cues of adults, 14 using rope-dragging methods, and 52 were incidental finds while observers were conducting other fieldwork. 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 person-hours. 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.

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 chicks 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 9). Other causes included weather, farming operations (crop only), and abandonment. Brown-headed cowbird (*Molothrus ater*) parasitism rates were 1.8% of nests on crop sites and 7.8% on native sites.

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. 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 efforts slowed significantly in late-June – early-July and there was only one main peak in nest initiation (Fig 10). 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 10). 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 ± 0.005SE and estimated nest survival over the 26-day exposure period (DSR^{25}) was 0.236 ± 0.028.

Reproductive Output. – Relative nest density (±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 ± 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 11), 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.

Habitat Conditions

We observed significant differences in vegetation conditions between crop and native sites that varied across survey rounds (Fig 11). Visual obstruction reading (VOR) was strongly influenced by the interaction between habitat type and survey round; a model that included this interaction had virtually all support in both years of the study (AIC_c $w_i = 0.99$; Table 12). In 2020, we found evidence that VOR was significantly higher in crop sites during survey round 3 than in survey round 1 ($\beta = 3.09 \pm 0.51$) and was lower in native sites than crop sites during the third round ($\beta = -2.80 \pm 0.75$; Fig 11). VOR estimates (cm ± SE) changed from 0.81 ±1.42 during round 1 to 17.81 ±1.43 during round 3 in crop sites and from 1.95 ±1.51 to 2.61 ±1.46 in native sites. The change in crop VOR by round 3 during 2021 had lower magnitude ($\beta = 0.72 \pm 0.42$) but was still lower in native sites than crop sites by round 3 ($\beta = -1.60 \pm 0.59$; Fig 11).

VOR estimates (cm ± SE) in 2021 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 strongly influenced by the effect of habitat type. The top model, with full support, included the effect of habitat type in both 2020 ($\mathrm{AIC_c}$ $w_i = 0.85$) and 2021 ($\mathrm{AIC_c}$ $w_i = 0.88$; Table 12). Bare ground was significantly lower on native sites than crop sites during 2020 ($\beta = -2.03 \pm 0.49$SE) and 2021 ($\beta = -1.51 \pm 0.39$; Fig 11). Estimated bare ground coverage (% ± SE) in 2020 was 45 ±6 in crop fields and 10 ±4 in native sites. In 2021, estimated bare ground coverage was 42 ±6 in crop fields and 14 ±4 in native sites.

The top two models for litter coverage in 2020 included effects of habitat type and survey round and together had the majority of support ($\mathrm{AIC_c}$ $w_i = 0.84$). However, confidence intervals for the effect size of survey round overlapped zero and this parameter was considered uninformative. The top model for 2021 contained an effect of habitat type ($\mathrm{AIC_c}$ $w_i = 0.66$; Table 12). Litter coverage was lower in native sites than crop sites in 2020 ($\beta = -1.31 \pm 0.52$) and 2021 ($\beta = -1.10 \pm 0.44$; Fig 11). Estimated litter coverage (% ± SE) in 2020 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.

The top model for litter depth both years included the interaction of habitat and survey round. This interaction model carried the majority of support in 2020 ($\mathrm{AIC_c}$ $w_i = 0.84$) and in 2021 ($\mathrm{AIC_c}$ $w_i = 0.94$; Table 12). In 2020, we found evidence that litter depth was initially lower in native sites than crop sites ($\beta = -1.08 \pm 0.39$) and decreased significantly in crop fields as the season progressed (round 2: $\beta = -0.99 \pm 0.37$; round 3: $\beta = -2.09 \pm 0.37$; Fig 11). Estimates (mm ± SE) changed from 4.66 ±1.30 during round 1 to 0.58 ±1.31 during round 3 in crop sites and from 1.57 ±1.34 to 1.05 ±1.32 in native sites. In 2021, this variable followed a similar pattern. We found evidence that litter depth was initially lower in native sites than crop sites ($\beta = -1.00 \pm 0.15$) and decreased in crop fields as the season progressed (round 2: $\beta = -0.67 \pm 0.15$; round 3: $\beta = -0.71 \pm 0.15$; Fig 11). Estimates (mm ± SE) changed from 2.75 ±1.12 during round 1 to 1.35 ±1.12 during round 3 in crop sites and from 1.01 ±1.12 to 0.91 ±1.12 in native sites.

For models of residual, forb, and grass cover, the null model was the best supported model in all analyses over both years ($\Delta AIC_c \leq 2$; Table 12) indicating 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).

Discussion

Collectively, our results do not support the hypothesis that crop fields are ecological traps for breeding thick-billed longspurs because: 1) settlement patterns of singing male longspurs 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 sites, and 2) nest survival, average clutch size, and the number of young fledged were similar between crop and native sites, providing no evidence for lower reproduction in crop sites. Additionally, precipitation and associated vegetation growth appeared to mediate longspur abundance and use of crop sites. Longspur abundance decreased throughout the breeding season in crop fields during a wet year (2020) as plant biomass increased whereas abundance did not change 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. Finally, 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 appear to shift timing of nesting in crop sites, perhaps allowing them to complete nesting efforts before crops grow and habitat becomes unsuitable late in the season. Based on our results, crop sites may benefit thick-billed longspur populations in northern Valley County, Montana by expanding nesting opportunities in an area where native habitat is limited.

Crop Fields as Potential Traps

The settlement of crop sites prior to native sites by longspurs, coupled with low reproductive success in crop sites, would lend support to the ecological trap hypothesis. Selection of native sites prior to crop sites, coupled with low reproductive success, would imply crop sites were sink habitats. If longspurs select territories based on habitat cues and crop sites contain preferred cues, then longspurs should exhibit preference for crop habitat (Delibes et al. 2001, Abrams et al. 2012, Hale and Swearer 2016). We observed similar settlement patterns of breeding territories in crop and native sites, indicating that selection cues and preference of longspurs were similar between habitat types. Although 50% of our study plots were occupied prior to deployment of song meters in early April, increases in daily longspur occupancy were similar across habitat strata and all sites were occupied by 27 April. In addition, our effort-adjusted estimate of nest density was 29% lower in crop sites than in native sites, though estimated precision was low and confidence intervals overlapped. Together, these findings suggest similar preference of longspurs for both crop fields and native rangeland.

Reproductive output, evaluated via nest survival, average clutch size, and the number of young fledged per successful nest, was similar across habitat types. Although we observed higher early nest failures in crop sites as a result of farming activities (e.g., seeding, disking, and plowing), thick-billed longspurs are quick to renest and often renested close to their failed first nest locations (Mickey 1943, Felske 1971, With 2021). While the most common cause of nest failure on both site types was predation, higher predation rates on native sites resulted in overall similar nest survival rates (~24%) across habitat types. 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 occur below the soil surface so that the top of the nest is level with the ground; farming activities such as rolling that did not disturb the soil did not negatively affect nests (n=9) regardless of whether they contained eggs or nestlings.

Most of our crop fields were sprayed with herbicides (Roundup™, 2-4D) twice per season and ≥5 fields were also sprayed once with organic fertilizers. Herbicide application consisted of a pre-spray to eliminate weeds around the time of seeding and a second application in June when plants were 5–6 inches tall (M. Sather, USFWS, pers. comm.). Although eggs and nestlings were sprayed, this did not directly result in nest or chick losses. However, we did not assess potential indirect effects of herbicide and fertilizer spraying on chick growth rates or subsequent fledgling 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 events, brown-headed cowbird parasitism, and possibly frequent disturbance by predators or perceived predators. On a few occasions in native sites (n=3), we found dead or near-dead nestlings apparently uninjured but laying on the ground outside the nest. We never observed any of these nestlings returned to the nest by adult longspurs and suspect this to be the activity of brown-headed cowbirds or other avian nest predators (Pietz and Granfors 2000, Pietz et al. 2012).

A broader demographic analysis including seasonal adult and post-fledging survival rates would increase our ability to discern which specific populations may be ecological traps, sources, or sinks. Our estimates of nest survival for thick-billed longspurs are similar to those reported in other studies, including studies of similar species such as horned lark (*Eremophila alpestris*) and chestnut collared longspur (Sedgwick 2004, Mahoney and Chalfoun 2016, Gaudet et al. 2020, Pulliam et al. 2021, Reintsma et al. 2022). While demographic data are exceedingly sparse for thick-billed longspur, our estimates of the number of young fledged per successful nest were also similar to those reported elsewhere (Sedgwick 2004, Lloyd and Martin 2005, Gaudet et al. 2020). Because the species will double-brood, a more meaningful measure of reproductive success would be seasonal fecundity, or the number of chicks produced per female in a season. To better understand mechanisms driving longspur population declines, we recommend conducting a complete evaluation of vital rates across life stages and assessing variation among years and habitat types. Estimates of adult and post-fledging survival are critical for understanding seasonal fecundity but require marking of individual birds. Importantly, these vital rate estimates may be complicated if females move between site types within a single season and attempt nests in both crop and native sites within a single year.

Recruitment coupled with adult survival determines population trajectories; to obtain estimates of recruitment and population growth between years, estimates of both adult and juvenile survival during migration and winter are also needed. However, low site fidelity in breeding areas makes estimation of these vital rates difficult for longspurs (Sedgwick 2004, With

2021). This lack of information precludes formal assessments of population viability and vital rate sensitivities of the species. However, populations of other grassland birds are highly sensitive to variation in adult survival (Sedgwick 2004, Perlut et al. 2008). Another sensitivity analysis of multiple species indicated that post-fledging survival rates of less than 0.4 required unrealistic overwinter survival of juveniles for most species unless adult survival and seasonal fecundity were extremely high (Cox et al. 2014). Recent advancements in VHF technology (e.g., Motus Wildlife Tracking System, Birds Canada, Ontario, Canada) may allow for expanded assessments of seasonal fecundity and annual survival of both adults and juveniles.

Evaluating body condition of fledglings, juveniles, and adult longspurs in crop sites would provide additional insight on habitat quality. Body condition at the start of migration often influences survival of adults and juveniles during migration and winter (Merilä and Svensson 1997, Angelier et al. 2011, Labocha and Hayes 2012). Lower post-fledging survival in crop sites, reduced body condition of adults or young, or lower seasonal fecundity of females nesting in crop sites would provide evidence for lower habitat quality of crop sites.

Longspur Abundance and Use of Crop Fields

Precipitation and vegetation structure appeared to mediate longspur abundance in crop sites but not native sites. Longspur abundance was relatively stable throughout the season in 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 in crop sites during a drought year (2021) when crop growth was stagnant. Because rates of nest abandonment were low across time and space, 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 because we did not mark birds.

During both years, we observed large flocks of non-breeding longspurs moving among crop sites. This behavior began around mid-late June and continued into July. Counts of singing males on these plots would increase to 3 – 5 times that of previous counts, and flocks typically moved elsewhere before the next survey round. This was a common occurrence on crop sites mid-season. It would be useful to have more information from tagged individuals in these flocks; we do not know if these are non-breeders or failed breeders that previously held territories on either crop or native sites.

Longspurs used all types of crop fields, including lentil, pea, flax, wheat, canola, mixed cover crop, and summer fallow. Although we didn’t have enough summer fallow plots (*n* = 12) to include this as a separate category in our analyses, we consistently observed lower longspur numbers in summer fallow fields compared to other crop types. Although one study found higher songbird abundances in summer fallow fields compared to other crop types (Martin and Forsyth 2003), we did not find this to be the case at our study site. 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, summer fallow fields are plowed multiple times during the breeding season. 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.

Timing of Nesting

In native habitats, longspurs are known to 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 sites than native sites throughout the breeding season, and exposed soils warm faster than vegetated soils (Song et al. 2013). We suspect that earlier warming of crop sites may generate an earlier invertebrate food supply and flocks of migrating longspurs may use crop fields as feeding grounds on their way north. In addition, median nest initiation dates during both years occurred 6–11 days earlier in crop sites than in native sites. Thus, earlier warming may allow earlier nest initiation and egg laying in crop sites. However, we did not assess thermal or other microclimatic conditions at nests, and we recommend collecting this information in future studies. In addition, the range of nest initiation dates and therefore length of nesting period was significantly shorter during the drought year. Longspurs are known to forego nesting or experience lower reproductive success during periods of extreme drought (Felske 1971, Shaffer et al. 2019). We observed a shorter nesting period in both crop and native sites during 2021. 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 extreme drought.

Conclusion

Thick-billed longspurs used crop fields in northeastern Montana, but we found no clear preference for crop sites over native and season-long reproduction was not reduced in crop sites.

Perhaps at a regional level where native habitat can be limited for longspurs, crop fields are beneficial to populations because they expand nesting opportunities at the landscape level. While hazards for ground nests may differ between crop and native sites, when comparing season-long reproductive effort, crop sites do not appear to be of very low quality. It appears that crop sites provide more opportunities for nesting and may support higher population levels than could be supported by existing native sites in this region alone. However, it is important to note that our study area contained large tracts of both crop and native habitats for thick-billed longspur (Fig 3); we have not assessed longspur use of crop landscapes without nearby native habitat.

Management Recommendations

Crop fields provided useable breeding and nesting habitat for thick-billed longspurs at our study area in Valley County, Montana. Though overall nest survival rates were similar to those in native sites, reproductive output can be improved with modified farming practices that minimize the destruction of nests. We recommend that farmers seed fields as early as possible, prior to 10 May, to minimize nest losses. Eliminating summer fallow farming practices may potentially benefit longspurs; this crop type appeared to be used infrequently and may present more hazards for nests as these fields are disked repeatedly throughout the summer. Pesticides and fungicides are known to harm both adult birds 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 the potential negative consequences of herbicide application on the survival of nesting longspurs can be evaluated.

The loss of native grasslands through conversion to cropland is considered one of the primary drivers of grassland bird population declines, including the thick-billed longspur

(Samson et al. 2004, Blann 2006, Ellis et al. 2010, Wright and Wimberly 2013). The Montana Partners for Fish and Wildlife Program (PFW) has begun implementing grassland restoration projects through private landowner agreements that focus on restoring marginal croplands back to native prairie (M. Sather, USFWS, pers. comm.). Restoration will no doubt provide benefits to grassland bird populations as it increases habitat area and reduces fragmentation, but benefits to thick-billed longspurs will depend on the seed mix used and soil type at restored sites. If restoration produces vegetative conditions that are too tall and dense for thick-billed longspur, this species will not use these restored sites. Our results suggest that longspurs would be more likely to use crop fields planted in a short-stature annual crop or sparsely vegetated cover crop.

TABLES

Table 1. Covariates used to model detection probability, initial occupancy, and settlement probability of thick-billed longspur in Valley County, Montana during the month of April in 2020 and 2021. The mean and range for each variable are shown as well. Time and day covariates were scaled prior to model fitting.

Model Covariates	**Description**	**Mean**	**Range**
Detection			
Precip	Level of daily precipitation (cm)	0.01	0.00 – 0.18
Mintemp	Minimum daily temperature (°F)	22.8	5.6 – 38.4
Time	Minutes past sunrise at start of recording	61	-26 – 153
Day	Julian day	108	97 – 120
Initial Occupancy			
Habitat	Habitat type	–	Crop, Native
Settlement			
Day	Julian day	108	97 – 120
Habitat	Habitat type	–	Crop, Native

Table 2. Covariates used to model detection, initial abundance, and seasonal trends of thick-billed longspur populations in Valley County, Montana from May-July, 2020–21, with a description of each. Start and wind covariates were scaled prior to model fitting.

Model Covariates	**Description**
Detection	
Obs	Observer (groups 1 and 2; ‘high’ and ‘low’ detection probability)
Temp	Temperature (°C) at start of survey
Start	Survey start time (minutes from sunrise)
Wind	Wind (km/hour)
Initial Abundance & Trend	
Habitat	Habitat type (‘crop’ or ‘native’)

Table 3. Candidate model set assessing the effects of covariates on daily nest survival rate (DSR) in Valley County, Montana, 2020–21.

Model	**Description**
Mod1	S(.)
Mod2	S(Habitat)
Mod3	S(Year)
Mod4	S(Initiation Date)
Mod5	S(Initiation Date + Initiation Date^2)
Mod6	S(log(Initiation Date))
Mod7	S(Habitat + Year)
Mod8	S(Habitat × Year)
Mod9	S(Habitat + Initiation Date)
Mod10	S(Habitat × Initiation Date)
Mod11	S(Year + Initiation Date)
Mod12	S(Year × Initiation Date)
Mod13	S(Habitat + Year + Initiation Date)
Mod14	S(Habitat × Year × Initiation Date)
Mod15	S(Habitat × log(Initiation Date))

Table 4. Candidate model set assessing the effect of habitat type (crop or native) and nest initiation date on the number of chicks fledged per successful nest in Valley County, Montana, 2020–21.

Model	**Description**
Mod1	Habitat × Initiation Date
Mod2	Habitat + Initiation Date
Mod3	Habitat
Mod4	Initiation Date
Mod5	Null

Table 5. Candidate model set assessing the effect of habitat type (crop or native) and survey round (1–3) on vegetation response within thick-billed longspur nesting habitat in Valley County, Montana, 2020–21. The same candidate model set was used for each measured habitat response variable.

Model	**Description**
Mod1	Habitat × Survey Round
Mod2	Habitat + Survey Round
Mod3	Habitat
Mod4	Survey Round
Mod5	Null Model

Table 6. 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, $\Delta QAIC_c$ values, and model weights ($QAIC_cWt$) are reported.

Model	**K**	**$QAIC_c$**	**$\Delta QAIC_c$**	**$QAIC_cWt$**
Detection				
$Time^2$ + 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
Initial Occupancy				
Null	9	834.02	0.00	0.98
Habitat	10	842.15	8.13	0.02
Settlement				
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 7. 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 8. 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, $\Delta QAIC_c$ values, and model weights ($QAIC_cWt$) are reported.

Model	**K**	**$QAIC_c$**	**$\Delta QAIC_c$**	**$QAIC_cWt$**
Detection 2020				
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
Initial Abundance, Trend 2020				
N(Habitat)γ(Habitat)	8	994.99	0.00	0.91
N(Habitat)γ(.)	7	999.56	4.56	0.09
N(.)γ(Habitat)	7	1010.00	15.01	0.00
N(.)γ(.)	6	1010.17	15.18	0.00
Detection 2021				
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
p(Obs + Wind + Temp + $Start^2$)	10	1303.81	9.43	0.00
Initial Abundance, Trend 2021				
N(.)γ(.)	6	1294.38	0.00	0.54
N(.)γ(Habitat)	7	1295.94	1.56	0.25
N(Habitat)γ(.)	7	1297.08	2.70	0.14
N(Habitat)γ(Habitat)	8	1298.68	4.30	0.06

Table 9. 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.

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

[a] Abandonment often occurred after weather or partial predation events in both site types.

[b] Weather events included flooding, hail, or storm damage which resulted in nest destruction or destruction of nest contents.

Table 10. 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 date^2, year, and habitat type (crop, native). The number of parameters (K), AIC$_c$ values, ΔAIC$_c$ values, and model weights (AIC$_c$Wt) are reported.

Model	**K**	**AIC$_c$**	**ΔAIC$_c$**	**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 11. 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$_c$Wt) are reported.

Model	**K**	**AIC$_c$**	**ΔAIC$_c$**	**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 12. Support for candidate models predicting differences in specific vegetation conditions in habitats used by thick-billed longspur in Valley County, Montana, 2020–21. Included are effects of habitat type (*habitat*; crop or native) and survey round (*round*; 3 rounds per season). The number of parameters (K), AIC$_c$ values, ΔAIC$_c$ values, model weights (w_i), and cumulative model weights (Cum w_i) are reported.

2020	**K**	**AIC$_c$**	**ΔAIC$_c$**	**w_i**	**Cum w_i**	**2021**	**K**	**AIC$_c$**	**ΔAIC$_c$**	**w_i**	**Cum w_i**
ln(VOR) ~						**ln(VOR) ~**					
habitat × round	7	549.95	0.00	1.00	1.00	habitat × round	7	613.56	0.00	1.00	1.00
round	4	563.37	13.42	0.00	1.00	round	4	630.12	16.56	0.00	1.00
habitat + round	5	565.52	15.57	0.00	1.00	habitat + round	5	631.68	18.11	0.00	1.00
Null	2	581.90	31.94	0.00	1.00	Null	2	632.73	19.16	0.00	1.00
habitat	3	583.96	34.01	0.00	1.00	habitat	3	634.18	20.62	0.00	1.00
bare ground ~						**bare ground ~**					
habitat	2	118.21	0.00	0.85	0.85	habitat	2	133.12	0.00	0.88	0.88
habitat + round	4	121.91	3.70	0.13	0.98	habitat + round	4	137.43	4.31	0.10	0.99
habitat × round	6	126.20	8.00	0.02	1.00	habitat × round	6	141.60	8.47	0.01	1.00
Null	1	153.34	35.14	0.00	1.00	Null	1	159.54	26.41	0.00	1.00
round	3	156.94	38.73	0.00	1.00	round	3	163.76	30.63	0.00	1.00
litter cover ~						**litter cover ~**					
habitat + round	4	79.40	0.00	0.51	0.51	habitat	2	90.25	0.00	0.66	0.66
habitat	2	80.32	0.91	0.33	0.84	habitat + round	4	92.46	2.22	0.22	0.88
habitat × round	6	82.32	2.91	0.12	0.96	Null	1	95.12	4.87	0.06	0.94
round	3	85.41	6.00	0.03	0.98	habitat × round	6	95.77	5.52	0.04	0.98
Null	1	86.24	6.84	0.02	1.00	round	3	97.34	7.09	0.02	1.00
ln(litter depth) ~						**ln(litter depth) ~**					
habitat × round	7	467.79	0.00	0.84	0.84	habitat × round	7	278.91	0.00	0.94	0.94
round	4	472.17	4.38	0.09	0.94	habitat + round	5	284.49	5.57	0.06	1.00
habitat + round	5	472.99	5.20	0.06	1.00	habitat	3	296.48	17.56	0.00	1.00
Null	2	488.50	20.71	0.00	1.00	round	4	324.78	45.87	0.00	1.00
habitat	3	489.27	21.48	0.00	1.00	Null	2	333.23	54.32	0.00	1.00
residual cover ~						**residual cover ~**					
Null	1	31.70	0.00	0.66	0.66	Null	1	78.95	0.00	0.70	0.70
habitat	2	33.84	2.14	0.23	0.89	habitat	2	81.53	2.59	0.19	0.89
round	3	35.89	4.19	0.08	0.97	round	3	83.12	4.17	0.09	0.97
habitat + round	4	38.10	6.40	0.03	1.00	habitat + round	4	85.76	6.82	0.02	1.00
habitat × round	6	42.44	10.74	0.00	1.00	habitat × round	6	89.92	10.97	0.00	1.00
grass cover ~						**grass cover ~**					
Null	1	93.14	0.00	0.63	0.63	Null	1	52.21	0.00	0.66	0.66
round	3	94.24	1.10	0.36	0.99	habitat	2	54.31	2.10	0.23	0.89
habitat	2	103.62	10.48	0.00	1.00	round	3	56.41	4.20	0.08	0.97
habitat × round	6	104.48	11.35	0.00	1.00	habitat + round	4	58.57	6.35	0.03	1.00
habitat + round	4	105.14	12.00	0.00	1.00	habitat × round	6	63.27	11.06	0.00	1.00
forb cover ~						**forb cover ~**					
Null	1	50.90	0.00	0.80	0.80	Null	1	24.09	0.00	0.67	0.67
round	3	54.04	3.14	0.17	0.96	habitat	2	26.39	2.30	0.21	0.89
habitat	2	57.58	6.68	0.03	0.99	round	3	28.22	4.13	0.09	0.97
habitat + round	4	60.84	9.94	0.01	1.00	habitat + round	4	30.57	6.49	0.03	1.00
habitat × round	6	62.09	11.19	0.00	1.00	habitat × round	6	34.90	10.82	0.00	1.00
grass (wheat only) ~						**grass (wheat only) ~**					
Null	1	88.23	0.00	0.62	0.62	Null	1	48.05	0.00	0.66	0.66
round	3	89.47	1.24	0.33	0.95	habitat	2	50.11	2.06	0.23	0.89
habitat × round	6	94.85	6.62	0.02	0.97	round	3	52.25	4.20	0.08	0.97
habitat	2	95.10	6.87	0.02	0.99	habitat + round	4	54.38	6.33	0.03	1.00
habitat + round	4	96.53	8.30	0.01	1.00	habitat × round	6	59.25	11.20	0.00	1.00

FIGURES

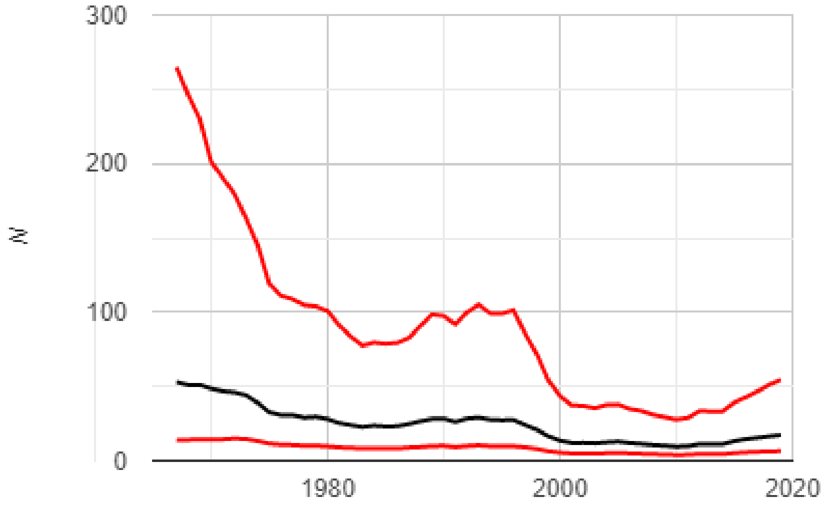

Figure 1. Estimated decline of thick-billed longspur populations based on Breeding Bird Survey data from 1966 – 2019 (Sauer et al. 2020). Estimated population size is shown on the y-axis and years are shown on the x-axis. Outer lines indicate estimated 95% confidence intervals.

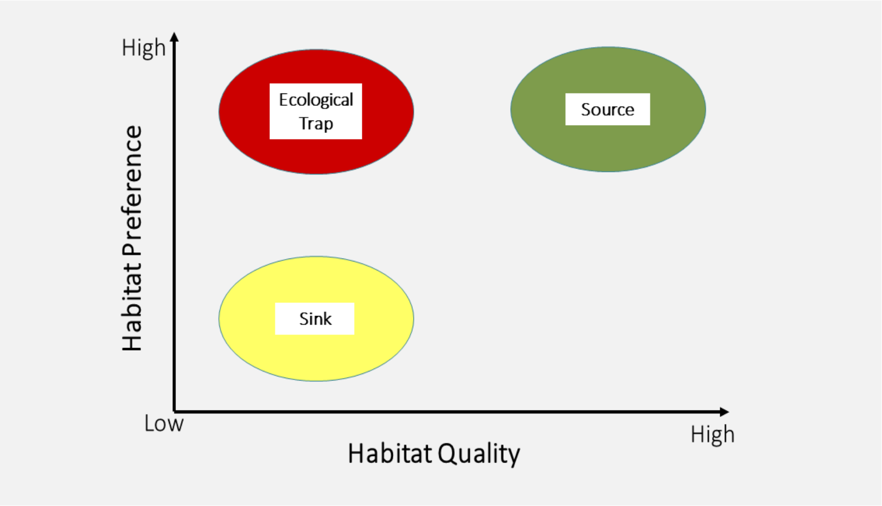

Figure 2. Conceptual diagram of ecological traps in the context of metapopulation theory. An ecological trap occurs when a habitat type is strongly preferred but habitat quality is low, resulting in reduced demographic rates. Metapopulations typically consist of sources (high preference, high quality), and sinks (low preference, low quality), but ecological traps can lead to maladaptive selection with such habitats operating as “preferred sinks”.

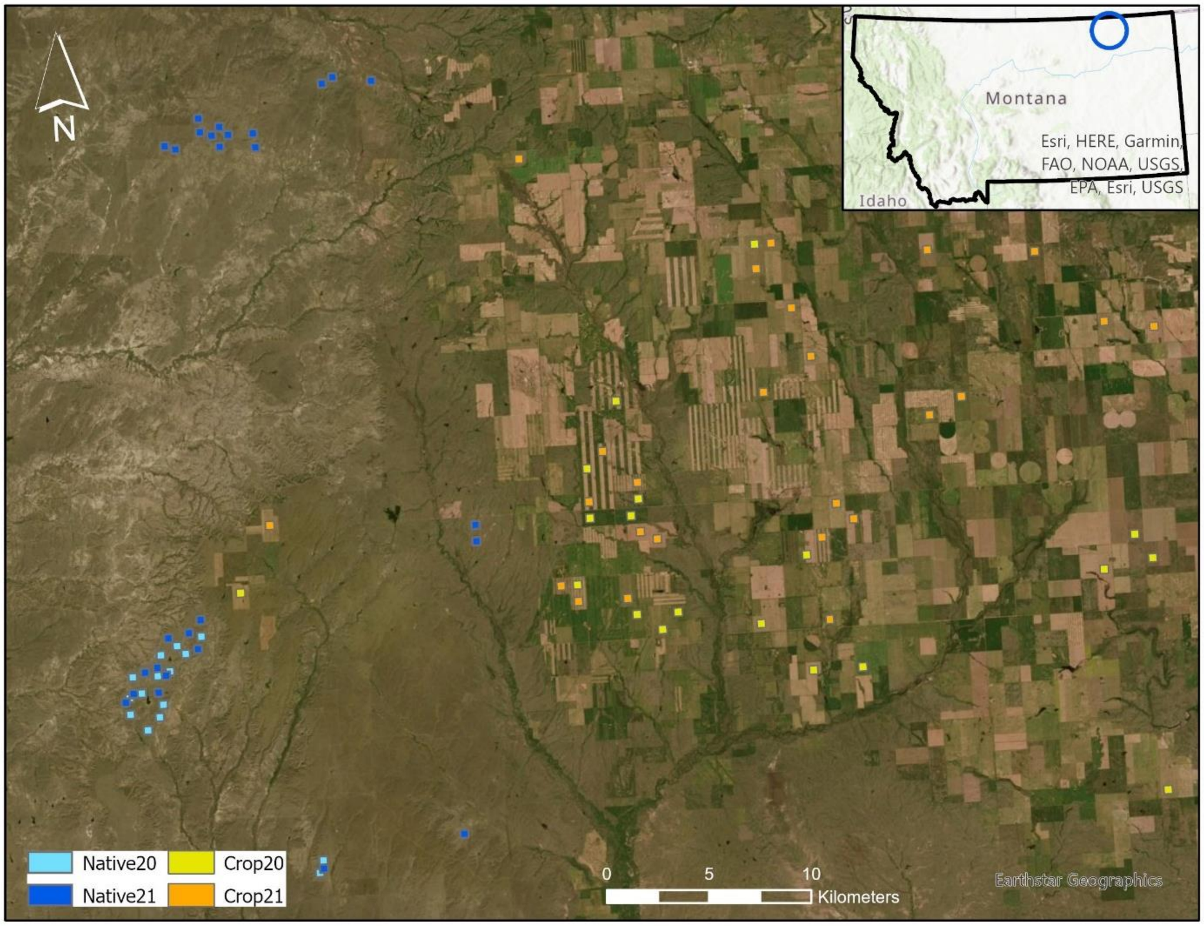

Figure 3. Map of study area and study plots on crop and native habitat sites in Valley County, Montana, 2020–21. Clustering of native plots is due to patchy distribution of thick-billed longspurs in native habitats.

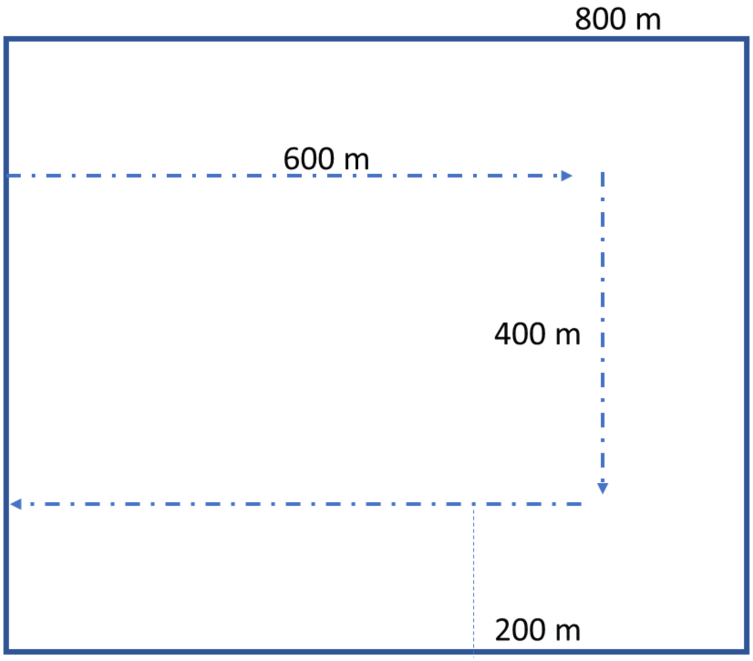

Figure 4. Conceptualization of layout of initial breeding bird survey transects in Valley County, Montana, 2020–21. The blue dashed line indicates the transect walked and the outer edge represents the survey plot.

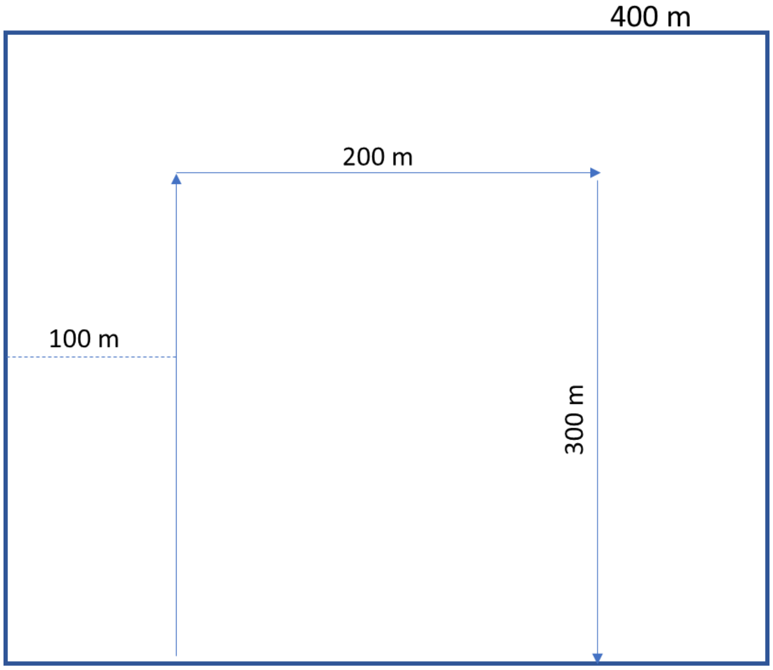

Figure 5. Conceptualization of layout of line transect surveys in Valley County, Montana, 2020–21. The blue lines with arrows represent the transect walked and the outer edge represents the survey plot.

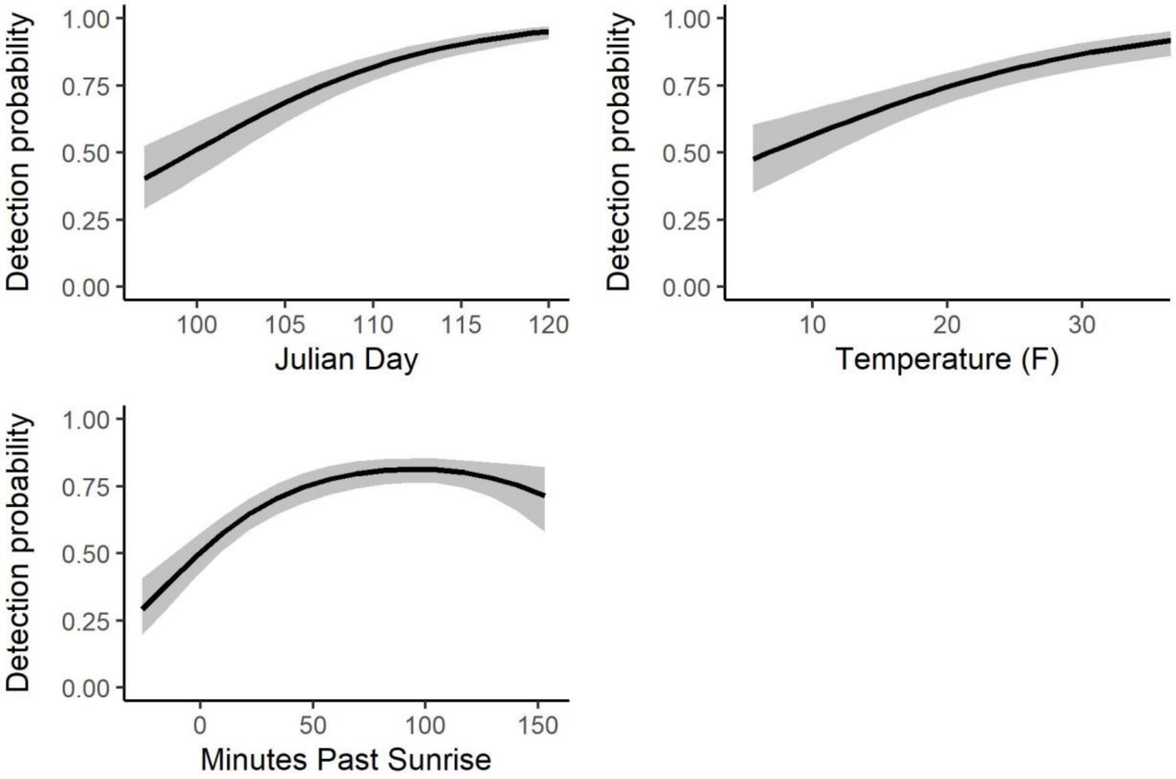

Figure 6. Estimated probability of detecting a thick-billed longspur on a song meter recording relative to Julian day (top left), daily minimum temperature (top right), and minutes past sunrise (bottom) in Valley County, Montana, during the month of April 2020–21. Shaded regions depict 95% confidence intervals.

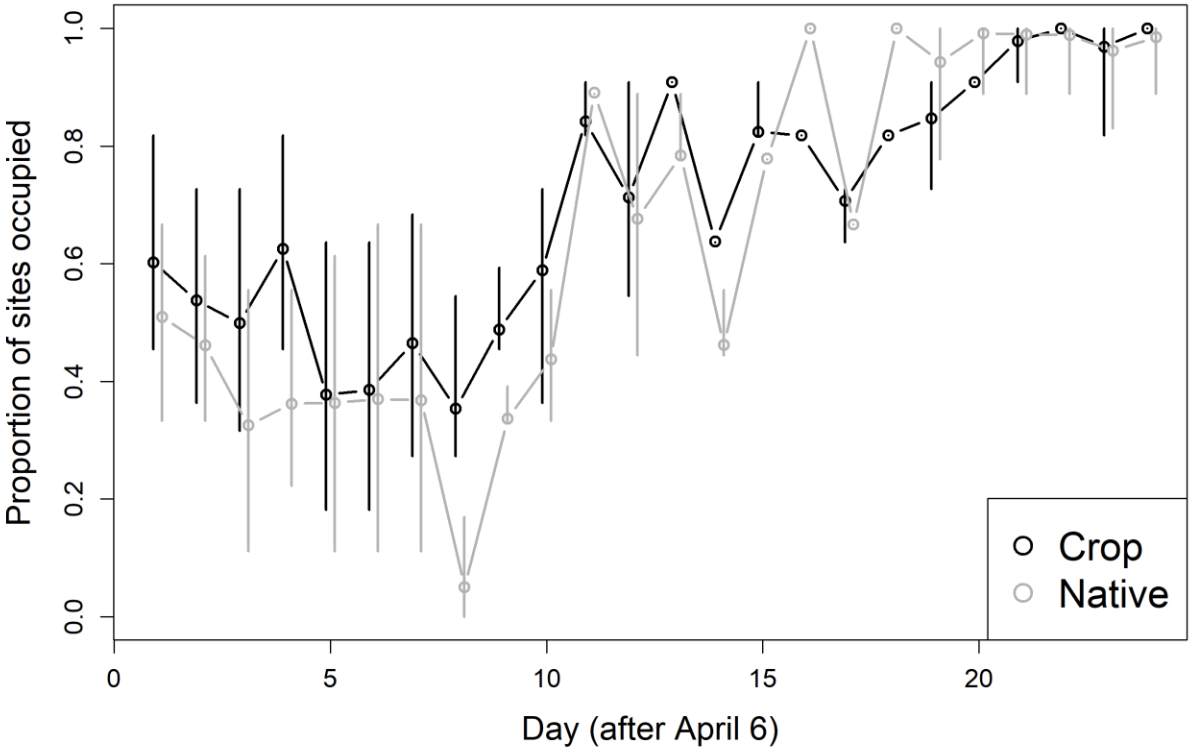

Figure 7: Estimates of latent occupancy (proportion of sites occupied by thick-billed longspurs) in both crop and native sites in Valley County, Montana, from 7 April – 30 April in 2020 and 2021. Whiskers indicate 95% confidence intervals.

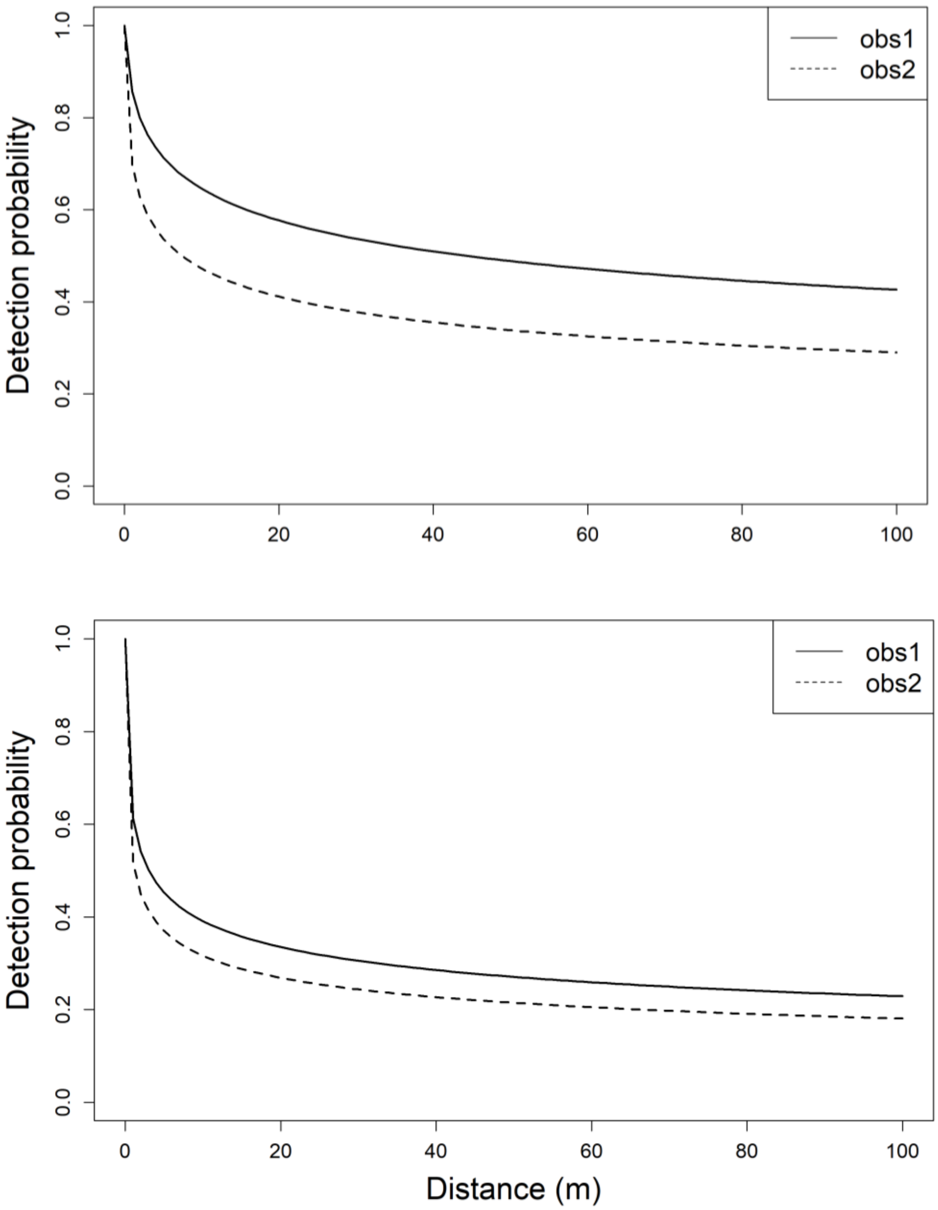

Figure 8. Effect of observer group (1 = high detection, 2 = low detection) on the distance detection function for thick-billed longspur surveys conducted in 2020 (top) and 2021 (bottom).

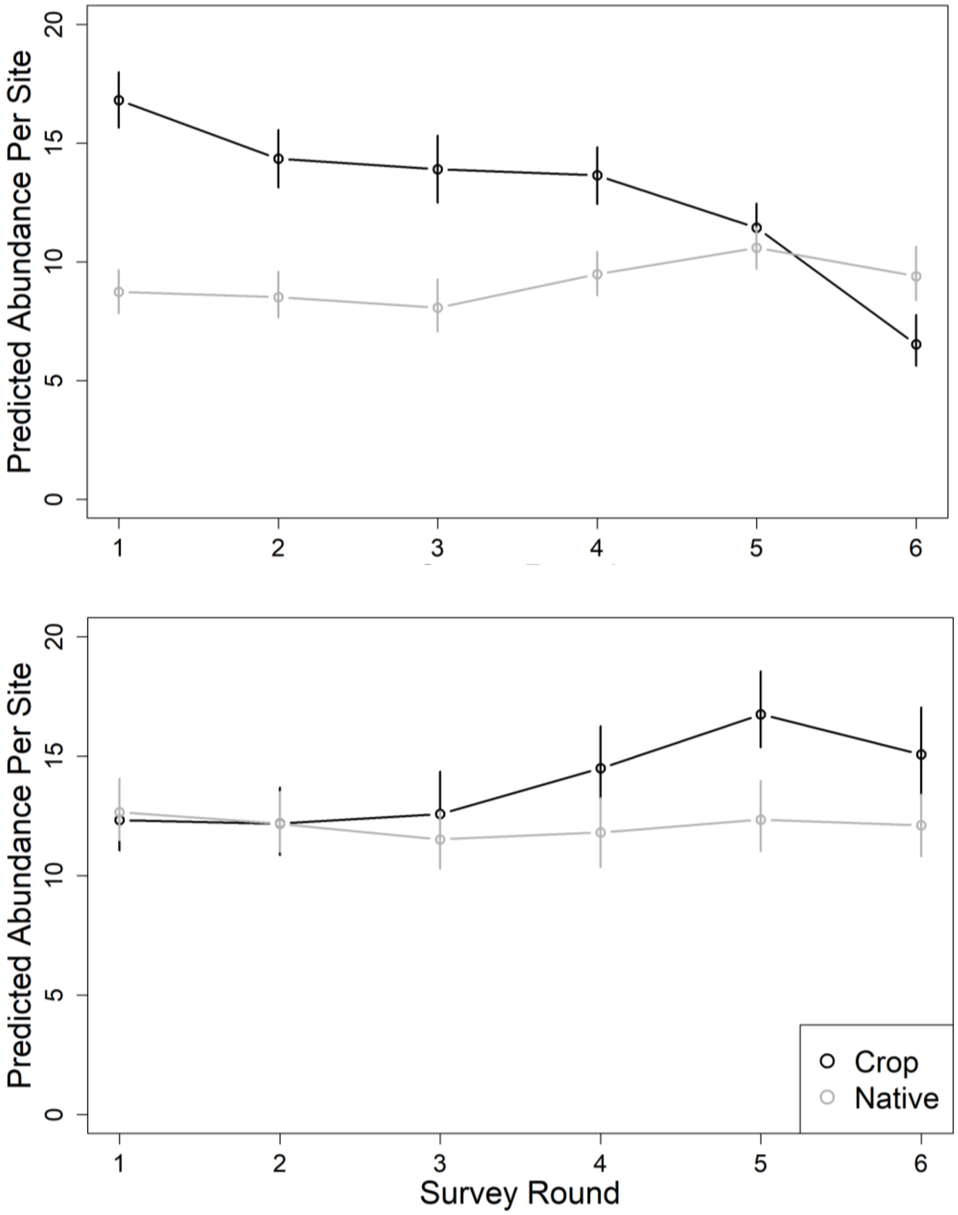

Figure 9. Empirical Bayes estimates of mean site-level abundance of thick-billed longspurs in both crop and native sites in Valley County, Montana, 2020 (top) and 2021 (bottom). Whiskers depict 95% confidence intervals. Survey rounds were evenly spaced between 10 May – 15 July each year.

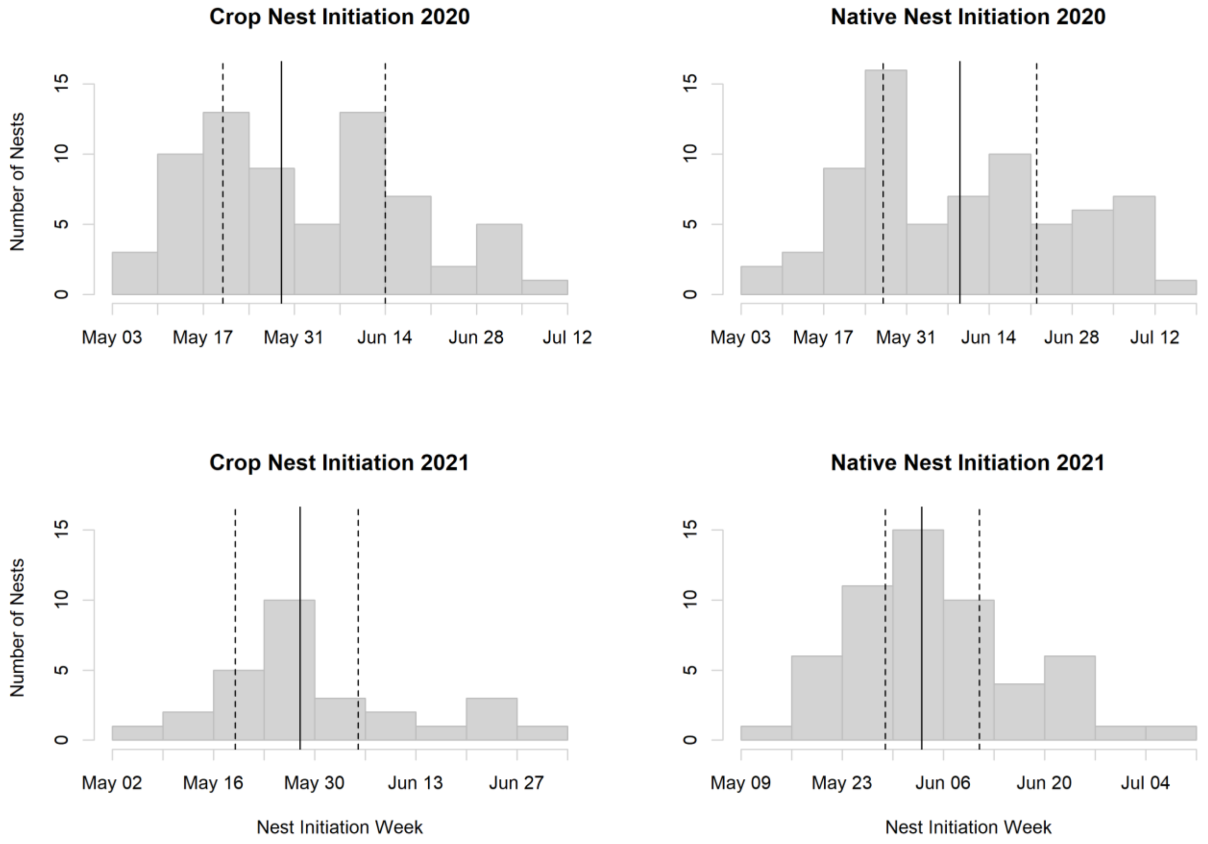

Figure 10. Estimated nest initiation dates in both crop and native sites for 222 thick-billed longspur nests found in Valley County, Montana, 2020–21. Results are based on 139 nests in 2020 (68 crop, 71 native) and 83 nests in 2021 (28 crop, 55 native). Overall nest initiation patterns were similar between crop and native sites given the year; 2020 was relatively cool and wet and 2021 was a drought year.

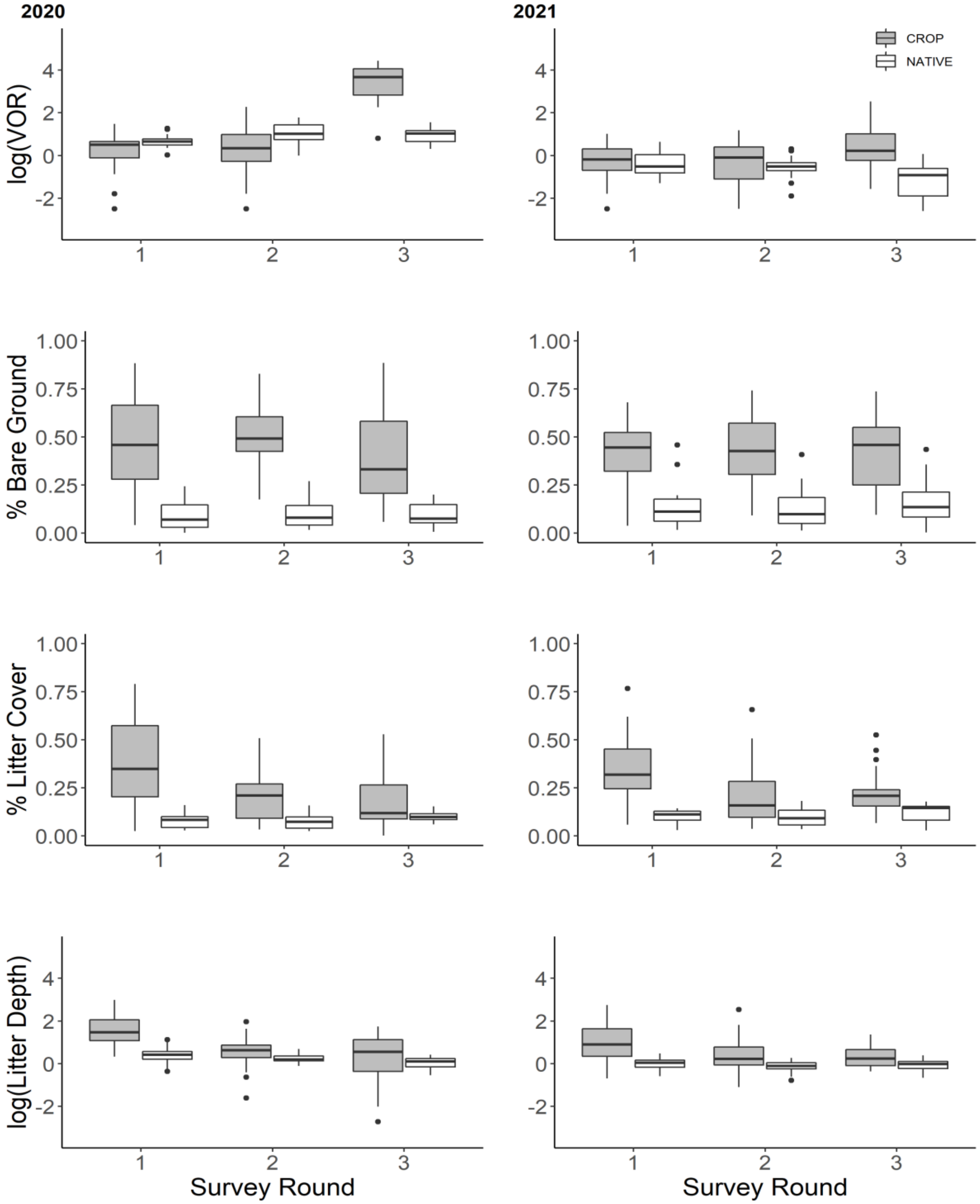

Figure 11. Differences in habitat conditions between crop and native sites and changes in conditions over the growing season (May, June, and July, survey rounds 1–3) for four habitat measures collected in northern Valley County, Montana, 2020–21. Measured variables include visual obstruction reading (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.

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.

Augustine, D. J., and B. W. Baker. 2013. Associations of grassland bird communities with black-tailed prairie dogs in the North American Great Plains. Conservation Biology 27:324-334.

Basore, N. S., L. B. Best, and J. B. Wooley Jr. 1986. Bird nesting in Iowa no-tillage and tilled cropland. The Journal of Wildlife Management 50:19-28.

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. 1986. Conservation tillage: ecological traps for nesting birds? Wildlife Society Bulletin (1973-2006) 14:308-317.

Blann, K. 2006. Habitat in agricultural landscapes: how much is enough. A state-of-the-science literature review. West Linn, OR: Defenders of Wildlife.

Bollinger, E. K., P. B. Bollinger, and T. A. Gavin. 1990. Effects of hay-cropping on eastern populations of the Bobolink. Wildlife Society Bulletin (1973-2006) 18:142-150.

Brennan, L. A., and W. P. Kuvlesky Jr. 2005. North American grassland birds: an unfolding conservation crisis? The Journal of Wildlife Management 69:1-13.

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.

Brown, A. D. 1891. The first record of McCown's Longspur breeding in Minnesota. Ornithology and Oology 16:142.

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.

Cox, W. A., F. R. Thompson III, A. S. Cox, and J. Faaborg. 2014. Post-fledging survival in passerine birds and the value of post-fledging studies to conservation. The Journal of Wildlife Management 78:183-193.

Currie, R. P. 1890. Notes from northern Minnesota. Oologist 7:206.

Dale, B. C., P. A. Martin, and P. S. Taylor. 1997. Effects of hay management on grassland songbirds in Saskatchewan. Wildlife Society Bulletin: 616-626.

Daubenmire, R. F. 1959. Canopy coverage method of vegetation analysis. Northwest Sci 33:39-64.

Davis, K. P., D. J. Augustine, A. P. Monroe, J. D. Derner, and C. L. Aldridge. 2020. Adaptive rangeland management benefits grassland birds utilizing opposing vegetation structure in the shortgrass steppe. Ecological Applications 30:e02020.

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.

Delibes, M., P. Ferreras, and P. Gaona. 2001. Attractive sinks, or how individual behavioural decisions determine source–sink dynamics. Ecology Letters 4:401-403.

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.

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.

Frawley, B. J., and L. B. Best. 1991. Effects of mowing on breeding bird abundance and species composition in alfalfa fields. Wildlife Society Bulletin (1973-2006) 19:135-142.

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., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns: we propose a paradigm that enhances heterogeneity instead of homogeneity to promote biological diversity and wildlife habitat on rangelands grazed by livestock. BioScience 51:625-632.

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.

Fuhlendorf, S. D., D. M. Engle, J. Kerby, and R. Hamilton. 2009. Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. Conservation Biology 23:588-598.

Fuhlendorf, S. D., W. C. Harrell, D. M. Engle, R. G. Hamilton, C. A. Davis, and D. M. Leslie Jr. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. Ecological Applications 16:1706-1716.

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.

George, T. L., A. C. Fowler, R. L. Knight, and L. C. McEwen. 1992. Impacts of a severe drought on grassland birds in western North Dakota. Ecological Applications 2:275-284.

Gill, F. B. 1990. Ornithology. 2nd ed. WH Freeman and Company, New York, NY, USA.

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.

Golding, J. D., and V. J. Dreitz. 2017. Songbird response to rest-rotation and season-long cattle grazing in a grassland sagebrush ecosystem. Journal of environmental management 204:605-612.

Green, J. C., and R. B. Janssen. 1975. Minnesota birds: where, when, and how many. University of Minnesota Press, Minneapolis, MN, USA.

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.

Grzybowski, J. A. 1982. Population structure in grassland bird communities during winter. The Condor 84:137-152.

Gundersen, G., E. Johannesen, H. Andreassen, and R. Ims. 2001. Source–sink dynamics: how sinks affect demography of sources. Ecology Letters 4:14-21.

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. Treml, and S. E. Swearer. 2015. Evaluating the metapopulation consequences of ecological traps. Proceedings of the Royal Society B: Biological Sciences 282:20142930.

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.

Howell, S. N., and S. Webb. 1995. A guide to the birds of Mexico and northern Central America. Oxford University Press.

Johnson, D. H., and L. D. Igl. 2001. Area requirements of grassland birds: a regional perspective. The Auk 118:24-34.

Johnson, M. D. 2007. Measuring habitat quality: a review. The Condor 109:489-504.

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.

Jonsomjit, D., S. L. Jones, T. Gardali, G. R. Geupel, and P. J. Gouse. 2007. A guide to nestling development and aging in altricial passerines.

Kéry, M., and R. Chandler. 2016. Dynamic Occupancy Models in Unmarked. https://mran.microsoft.com/snapshot/2017-06-27/web/packages/unmarked/vignettes/colext.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.

Klett, A. T., H. F. Duebbert, 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. 1994. Avian assemblages on altered grasslands. Studies in Avian Biology 15:247-257.

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.

Krause, H. 1968. The McCown's Longspur: A life history. Manila, Philippines: MDB Publishing House.

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.

Lockwood, J. A., and L. D. DeBrey. 1990. A solution for the sudden and unexplained extinction of the Rocky Mountain grasshopper (Orthoptera: Acrididae). Entomological Society of America 5:1194-1205.

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.

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.

MacRae, R. J., S. B. Hill, G. R. Mehuys, and J. Henning. 1990. Farm-scale agronomic and economic conversion from conventional to sustainable agriculture. Advances in agronomy 43:155-198.

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., and D. J. Forsyth. 2003. Occurrence and productivity of songbirds in prairie farmland under conventional versus minimum tillage regimes. Agriculture, ecosystems & environment 96:107-117.

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 (Métodos para localizar nidos y monitorear el éxito 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. Ells. 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.

Menendez III, H. M., M. R. Wuellner, B. L. Turner, R. N. Gates, B. H. Dunn, and L. O. Tedeschi. 2020. A spatial landscape scale approach for estimating erosion, water quantity, and quality in response to South Dakota grassland conversion. Natural Resource Modeling 33:e12243.

Merilä, 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.

Muller, J. A., and J. D. Ross. 2022. Fine-scale habitat associations of Oklahoma's longspurs. The Journal of Wildlife Management: e22258.

Murphy, M. T. 2003. Avian population trends within the evolving agricultural landscape of eastern and central United States. The Auk 120:20-34.

Nice, M. M. 1931. The birds of Oklahoma, revised edition. Publication of the Univ. Oklahoma, Biol. Sur. 3.

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.

Peterjohn, B. G. 2003. Agricultural landscapes: can they support healthy bird populations as well as farm products? The Auk 120:14-19.

Phillips, A. R., J. Marshall, and G. Monson. 1964. The birds of Arizona. University of Arizona Press.

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.

Remeš, V. 2003. Effects of exotic habitat on nesting success, territory density, and settlement patterns in the Blackcap (*Sylvia atricapilla*). Conservation Biology 17:1127-1133.

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.

Rodenhouse, N. L., and L. B. Best. 1983. Breeding ecology of vesper sparrows in corn and soybean fields. American Midland Naturalist: 265-275.

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.

Saunders, A. A. 1921. A Distributional List of the Birds of Montana: With Notes on the Migration and Nesting of the Better Known Species. The Club.

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., M. Burbach, L. Powell, and W. Schacht. 2018. Ranchers' perceptions of vegetation heterogeneity in the northern Great Plains. Great Plains Research 28:185-198.

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.

Smith, L. M., D. A. Haukos, and R. M. Prather. 2004. Avian response to vegetative pattern in playa wetlands during winter. Wildlife Society Bulletin 32:474-480.

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.

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.

Sutton, G. M. 1967. Oklahoma Birds, their Ecology and Distribution with Comments on the Avifauna of the Southern Great Plains. University of Oklahoma Press, Norman, OK, USA.

Taverner, P. A. 1927. Some recent Canadian records. Auk 44:217-228.

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 Oost, K., G. Govers, T. A. Quine, G. Heckrath, J. E. Olesen, S. De Gryze, and R. Merckx. 2005. Landscape-scale modeling of carbon cycling under the impact of soil redistribution: The role of tillage erosion. Global Biogeochemical Cycles 19.

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., J. R. Herkert, F. L. Knopf, J. Ruth, and C. E. Keller. 2000. Grassland birds: An overview of threats and recommended management strategies. Strategies for bird conservation: The Partners in Flight planning process:1-5.

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.

Weldon, A. J., and N. M. Haddad. 2005. The effects of patch shape on Indigo Buntings: evidence for an ecological trap. Ecology 86:1422-1431.

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.