

Management Recommendations for
Thick-billed Longspur
(*Rhynchophanes mccownii*)
in Montana



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Introduction

Conversion of native grassland to cultivated cropland remains one of the greatest threats to prairie ecosystems in North America (Ellis et al., 2010; Wright and Wimberly, 2013). Land conversion and intensification of agricultural practices are considered to be leading drivers of grassland bird population declines worldwide (Davis et al., 2020). The thick-billed longspur (*Rhynchophanes mccownii*) is a grassland specialist of conservation concern that breeds within the short- and mixed-grass prairies of eastern Montana. Thick-billed longspur populations have declined 4% annually since 1966, yet mechanisms driving the decline are poorly understood (Rosenberg et al., 2019; Sauer, 2020). Thick-billed longspurs have unique habitat preferences, opting for short, sparse vegetation with ample bare ground. This species exhibits low inter-annual philopatry, historically relying on vast landscapes and a shifting mosaic of natural disturbance patterns to maintain large patches of habitat suitable for nesting (Shaffer et al., 2019; With, 2021). Moreover, thick-billed longspurs are known to nest in cultivated fields (i.e., cereal and pulse crops; hereafter ‘crop fields’) in parts of their breeding range (Snyder and Bly, 2009; With, 2021).

Thick-billed longspur use of crop fields as nesting habitat has been investigated or mentioned in very few studies (Felske, 1971; Martin and Forsyth, 2003; Snyder and Bly, 2009; Davis et al., 2020). Consequently, little is known regarding population level impacts of nesting in crop fields. In Europe and North America, crop fields appear to be poor nesting habitat for many songbirds (Rodenhouse and Best, 1983; Frawley and Best, 1991; Dale et al., 1997) but beneficial to others, even expanding nesting opportunities in certain systems (Martin and Forsyth, 2003; Weintraub et al., 2016). While grassland bird biodiversity is substantially reduced in extensively cultivated landscapes, select species may prefer nesting in these habitats (Davis et al., 2020).

Ground-nesting birds face a myriad of hazards in fields which are tilled, disked, seeded, sprayed, and harvested one or more times during a breeding season; herbicide and pesticide use can harm birds through direct exposure or indirectly by limiting prey resources (Loss et al., 2015; Davis et al., 2020). Additionally, vegetation structure in crop fields changes rapidly and substantially as crops grow, altering habitat suitability during the nesting season (Wilson et al., 2005). Some birds prefer dense cover at the nest site and rely on it to conceal them from predators, but others, such as the thick billed longspur, rely more on their ability to detect predators and employ communal defense behaviors (With, 1994; Davis, 2003). While crop fields

may provide wide viewsheds early in the season, this changes rapidly as crops grow, which may lead to abandonment of territories and thus lost nesting opportunities late in the season (Devries et al., 2008). Vegetation also protects nests from weather extremes, with early nesting birds often utilizing shorter vegetation to take advantage of added warmth from sun exposure, whereas later nesting species often prefer denser vegetation to aid in thermoregulation during the warmer months (Felske, 1971; With, 1994; Wilson et al., 2005). We conducted a two-year study to assess use of crop fields by thick-billed longspurs during the nesting season (Swicegood et al., 2023). Here we offer some guidelines for managers stemming from this research, and we also demonstrate the uniqueness of thick-billed longspur habitat requirements.

Our Study

Our goal was to better understand how nesting in crop fields may impact thick-billed longspur populations by testing the hypothesis that crop fields operate as an ecological trap (Swicegood, 2022; Swicegood et al., 2023). We did this by comparing the following in crop fields and native grassland sites: 1) timing of territory establishment, 2) longspur abundance and changes in abundance over the breeding season, and 3) nest survival and fledgling production. Our fieldwork was conducted in northern Valley County, Montana, 2020–21, and this region lies within the core of the remaining breeding distribution of thick-billed longspurs (Sauer, 2020). Crop types included spring wheat, lentil, flax, pea, summer fallow (half planted in spring wheat), canola, and cover crop (e.g., a diverse seed mix planted to reduce erosion). Native grassland sites occurred on nearby private and federal grazed lands (Swicegood, 2022; Figure 1).

We found that the timing of territory establishment was similar in crop fields and native prairie during the month of April. Surprisingly, we also found that nest survival and number of fledglings produced per successful nest were similar in crop and native sites. Nest survival over the 26-day exposure period was 0.236 ± 0.028 SE and the number of fledglings produced per successful nest averaged 2.90 ± 0.18 SE in both site types (Swicegood et al., 2023). Thick-billed longspur abundance differed between crop and native sites during a non-drought year, but not substantially during a drought year. Abundance was more variable in crop fields, and during a non-drought year, decreased significantly over the season (ranging from ~16–6 estimated birds per plot) as plant biomass increased from 0.81 cm (± 1.56 SE) in May to 17.89 cm (± 1.58) in July, reaching a density unsuitable for longspurs. During a drought year, abundance increased marginally over the season in crop fields (range ~12–15 birds per plot) as plant biomass

remained low (0.72 cm [± 1.54] in May to 1.47 cm [± 1.54] in July). Longspur abundance was relatively stable in native sites during both years (estimated ~9 and 12 birds per plot in non-drought and drought years, respectively), although typically slightly lower than abundance in crop fields (Swicegood et al., 2023; Table 1).

Timing was critical for successful nesting in crop fields. Nests destroyed by farm equipment included those that overlapped with the seeding of fields early in the season and those that occurred in fallow portions of summer fallow fields which were tilled 2–3 times during a season. Harvest in northern Valley County occurred in August or September after longspurs had completed nesting. Other mechanical operations, including rolling and herbicide application, did not noticeably impact longspurs. Nest loss to farm machinery was relatively low, and other causes of nest failure included predation, abandonment, and weather, with predation rates being higher on native sites (Swicegood et al., 2023; Table 2).

Interestingly, during both years of our study, median nest initiation dates occurred 6–11 days earlier in crop fields than native sites (Figure 2). Because exposed soils warm faster than vegetated soils, it is possible that favorable microclimatic conditions or an earlier invertebrate food supply may allow earlier nest initiation and egg laying on crop sites (Felske, 1971; Greer and Anderson, 1989; Song et al., 2013). The season-long nesting period appeared to be abbreviated in crop fields during a non-drought year when longspurs began abandoning crop territories in July as vegetation biomass increased (6 nests found in crop fields after June 30, 11 on native sites), but this effect was less pronounced during a drought year as adult birds remained on crop territories. The nesting season appeared to be abbreviated during the drought year on both crop and native sites with only one nest being found after June 30 in native grassland and none in crop fields (Swicegood et al., 2023). However, these are anecdotal observations of longspur behavior, and the number of nests found after June 30 was also impacted by observer ability to detect nests, which was unaccounted for.

Management Recommendations

Coexisting with longspurs—Our study showed that longspurs were able to nest successfully in crop fields, with success rates comparable to nests in native grassland. Croplands have been shown to be important nesting habitat for other passerines (Best et al., 1995; Lokemoen and Beiser, 1997; Donald et al., 2006). Considering that croplands now occupy a vast portion of arable regions worldwide, it may be advantageous to encourage management of these

landscapes in ways that enhance nesting habitat for passerines. In particular, modifying the timing or degree of mechanical disturbance in cropland would provide direct benefits to ground-nesting birds. In our study, the greatest amount of nest destruction by farm equipment occurred early in spring during field seeding. The first peak in nest initiation occurred between 15 May and 1 June with nominal variability between the two years. We recommend early seeding (<10 May) when possible, to limit nest destruction by farm machinery. In addition, elimination of summer fallowing would benefit longspurs. Besides tilling or disking, the only other mechanical disturbances include spraying and potentially rolling (for lentil fields), neither of which directly destroyed nests. Summer fallow fields are the only crop type in which the soil is mechanically disturbed multiple times per season, and this can have disastrous consequences for birds that repeatedly attempt nesting in such fields. Alternatively, leaving portions of summer fallow fields truly fallow (i.e., not disturbing the soil), or planting a short-growing cover crop may improve nest survival for thick-billed longspurs. However, due to low abundance of longspurs in summer fallow fields compared to other crop types during our study (Swicegood, 2022; Swicegood et al., 2023), we suspect that longspurs use these fields less frequently due to either a) the presence of more abrupt edges, or b) a reduced invertebrate food supply or unfavorable microclimatic conditions. Summer fallow fields are planted in strips ranging from 250–400 m wide and many birds avoid habitats with increased edge amount (Johnson and Igl, 2001; Koper and Schmiegelow, 2006; Sliwinski and Koper, 2012). Repeated mechanical disturbance is known to degrade soil ecology and arthropod biodiversity (Stinner and House, 1990; Kladvko, 2001). Due to low use by longspurs and frequent human disturbance, summer fallow fields in this region are likely detrimental for thick-billed longspurs.

Many different types of pesticides and fungicides can harm adult and nestling passerines (McEwen and Ells, 1975; Martin et al., 1998; Mineau and Whiteside, 2013). Although we did not observe any direct mortalities or nest failures from herbicide application in crop fields, we still recommend reducing or eliminating widespread application of herbicides, pesticides, and fungicides when possible, until potential impacts on the survival of nesting longspurs can be evaluated. We encourage farmers to investigate alternative solutions for pest control.

While management for thick-billed longspurs in crop fields should be region-specific, creative solutions may provide additional benefits for a species utilizing such novel niche space resulting from landscape-level anthropogenic change (Wilson et al., 2005). For example,

Odderskær et al. (1997) found that artificially creating open areas (7 m²) within cereal fields resulted in higher skylark densities and extended nesting seasons. Provided that mechanical operations such as seeding and harvesting occurred at appropriate times, similar tactics may benefit thick-billed longspurs. Recent studies have indicated that autumn-seeded wheat, or winter wheat, benefits nesting waterfowl and numerous passerine species over spring-seeded wheat because it provides additional cover early in the breeding season and eliminates the need for spring tillage (Devries et al., 2008; Skone et al., 2016; Davis et al., 2020). Nevertheless, winter wheat is unlikely to provide nesting sites for thick-billed longspurs because these birds seek out bare ground and sparse vegetation during territory establishment. Thick-billed longspurs begin nesting early (in May) and likely take advantage of the added warmth provided by short vegetation structure in early spring (Felske, 1971). In addition, thick-billed longspurs rely on their ability to detect predators while incubating (With, 1994). Short vegetation allows longspurs to best exploit this niche space, and it is also hypothesized that longspurs may experience increased foraging efficiency in sparsely vegetated habitats if prey is more accessible (With, 2021). Furthermore, spring-seeded crops allow for a longer breeding season than autumn-seeded, as plants take longer to reach threshold height and density (Davis et al., 2020).

Thinking bigger—Grassland birds demonstrate low philopatry between years as habitat conditions across prairie landscapes shift as a consequence of unpredictable weather and disturbance regimes (Jones et al., 2007). Specifically, the thick-billed longspur has evolved to take advantage of these shifting patterns by following disturbances, sometimes shifting territories within a single season (Felske, 1971; With, 2021). Thick-billed longspurs consistently produce 2 nests per year in native grassland (Shaffer et al., 2019), and late nesting attempts may be lost in crop landscapes that become unsuitable. In one instance in 2020, we observed an influx of singing male longspurs into a newly disked field that had been planted in dense cover crop during May and June. Upon disking in early July, average counts increased from 1–2 birds per survey to 9–14 birds per survey and we found 3 new nests, accounting for half of the 6 nests found after June 30 in all crop fields that year. This occurred while average bird and nest densities in other fields (primarily spring wheat) decreased as plant biomass increased. It may be critical that the surrounding landscape contains enough short-stature crop types or suitable native grassland to support late nesting attempts from crop nesters after abandonment of initial territories. Maintaining a diverse array of crop types and vegetation structure across the

landscape will give longspurs opportunities to move and reneest when a particular field becomes unsuitable. Crops that grow at different rates and different times may impact how longspurs move around the landscape during breeding season.

We investigated longspur use of crop fields at the nest site and pasture level (16 ha), but not at landscape-level scales. Other studies have shown the importance of scale for understanding grassland bird habitat use (Best et al., 2001; Eggers et al., 2011). Lipsey et al. (2017) used a hierarchical modeling framework to evaluate bird response to local habitat conditions within a broader landscape context. They found that for Sprague's pipit (*Anthus spragueii*) and Chestnut-collared longspur (*Calcarius ornatus*), the amount of grass within the surrounding landscape (1492 km², quadrangle) influenced habitat selection at local scales (93 km², township; 2.6 km², section). These birds avoided apparently suitable habitat at local scales for which the surrounding landscape contained too little grassland. It is likely that thick-billed longspurs exhibit similar patterns and the use of croplands as nesting habitat may be limited to areas close to historical native prairie habitats or short-stature crop types, depending on habitat selection behavior at higher spatial scales (e.g., 1st order habitat selection; Johnson, 1980). Just as grassland bird management on native sites will benefit from considering species' requirements at multiple spatial scales (Lipsey et al., 2017), it is likely that the same will be true for grassland specialists nesting in croplands (Davis et al., 2020).

Native prairie restoration—Restoration of fallow croplands back to native grassland is a common management practice designed to benefit grassland birds and other wildlife (M. Sather, pers. comm.). However, limited information exists regarding the benefits of restoration and these areas often do not reflect the structure or diversity of native grassland (Fletcher and Koford, 2002). Therefore, we strongly recommend preservation of native prairie be prioritized over restoration of croplands, especially in core areas valuable to species of conservation concern, but restoration may have some utility in areas already under agricultural production. It is imperative that we design restoration plans that are region-specific, and resulting plant species composition, biomass, and vegetative structure must mimic the native prairies that we desire to recreate. While certain exotic species (e.g., crested wheatgrass [*Agropyron cristatum*], Kentucky bluegrass [*Poa pratensis*], and yellow sweetclover [*Melilotus officinalis*]) may establish quickly and minimize soil erosion, such species are invasive and are unlikely to shift to native vegetation (Wilson, 1989). Many grassland birds of conservation concern, including thick-billed longspur and the

similar chestnut-collared longspur, are less likely to use restored sites dominated by dense, exotic vegetation (Lloyd and Martin, 2005; Pulliam et al., 2020). Furthermore, the most arable lands in eastern Montana contain the most productive soils; therefore, properly restored croplands in this region should support highly productive native vegetation. Restoring such habitats may benefit other grassland birds (e.g., Sprague's pipit and Baird's sparrow) but are unlikely to be utilized by thick-billed longspurs. In such productive native grasslands, reinstating natural disturbance regimes such as fire and heavy grazing may improve nesting habitat for short-grass specialists (Fuhlendorf et al., 2006).

Quantifying Habitat Structure

We quantified vegetation characteristics of both crop and native sites used by thick-billed longspurs at our study site in northern Valley County, Montana (Swicegood, 2022; Swicegood et al., 2023). In this report, we include a summary of average vegetation conditions at the plot level (16 ha) and a list of the most abundant plant species found on native sites. We also surveyed 10 additional native plots in 2020 which were unoccupied by thick-billed longspurs, but occurred in proximity to occupied plots (minimum distance = 421 m, maximum = 6085 m, average = 3451 m) and appeared superficially similar. We conducted three rounds of vegetation surveys across each breeding season (May, June, and July). We surveyed 10 points per plot in native sites and 3 points per plot in crop sites during each round (Swicegood, 2022). We discuss whether vegetation conditions changed substantially over the season and if they differed between survey years, otherwise combined averages are reported (Tables 3–8). We used generalized linear models to test for year and survey round effects on each habitat variable; estimates are from the top model.

The most abundant plant species in occupied native plots were wheatgrass (*Elymus spp.*), prairie junegrass (*Koeleria macrantha*), Sandberg bluegrass (*Poa secunda*), blue grama (*Bouteloua gracilis*), spikemoss (*Selaginella spp.*), vagrant lichen (most likely *Xanthoparmelia spp.*), needle-and-thread (*Hesperostipa comata*), green needlegrass (*Nassella viridula*), pussytoes (*Antennaria spp.*), and fringed sagewort (*Artemisia frigida*). Other common species included western yarrow (*Achillea millefolium*), phlox (*Phlox spp.*), scarlet globemallow (*Sphaeralcea coccinea*), saltbush (*Atriplex spp.*), dandelion (*Taraxacum officinale*), woolly plantain (*Plantago patagonica*), upland sedge (*Carex spp.*), American vetch (*Vicia americana*), silver sagebrush (*Artemisia cana*), green rabbitbrush (*Chrysothamnus viscidiflorus*), broom snakeweed

(*Gutierrezia sarothrae*), desert parsley (*Lomatium sp.*), curlycup gumweed (*Grindelia squarrosa*), rockcress (*Arabis sp.*), and plains pricklypear (*Opuntia polyacantha*).

In native sites occupied by thick-billed longspur, grass cover averaged $36 \pm 6\%$ SE during the non-drought year and $16 \pm 4\%$ during the drought year. Bare ground cover averaged around 10–14% and litter cover was low ($<15\%$). Exotic plant cover (e.g., forb and grass non-native species) was also low ($<10\%$). Residual plant cover was $<40\%$, forb cover $<30\%$; forb cover was lower during the drought year and residual cover was higher during drought as vegetation dried out more rapidly. Other notable cover types included lichen (i.e., a vagrant lichen species of *Xanthoparmelia* genus; average 5–6% cover), spikemoss (*Selaginella spp.*; average 10–11% cover), and crust, which we called any dead, dried lichen that had turned black or other hard material that was not bare ground (average 18–21% cover; Table 3).

In native sites unoccupied by thick-billed longspur (year 2020 only, $n=10$ survey plots), grass cover appeared slightly higher than averages for occupied plots ($44 \pm 9\%$ SE). Bare ground cover was lower ($4 \pm 4\%$) and litter cover was higher ($21 \pm 8\%$). Exotic plant cover was marginally higher at $11 \pm 6\%$. Residual and forb cover were similar. Lichen cover was very low (1% cover), spikemoss appeared slightly lower (7% cover), and crust was marginally lower (16% cover) than estimates in occupied plots (Table 4). Shrub cover was ubiquitously low across the study area. Note that here we just report average estimates and sample sizes were vastly different between occupied and unoccupied plots; these are not true tests of statistical differences.

Grass and forb cover were lumped together as “plant cover” in crop fields. In these monocultures, one crop species was normally present and we disregarded whether vegetation structure consisted of forb or grass species. Plant cover increased drastically from May–July both years, but was more pronounced during the non-drought year (i.e., $4 \pm 4\%$ SE in May to $46 \pm 10\%$ cover in July). Bare ground cover was much higher in crop sites (average 42–45%) than native sites. Litter cover was also higher (average 36–37%) but decreased as the season progressed, particularly after fields were disked and residual material began breaking down. Residual cover was somewhat lower in crop fields (Table 5).

Notable differences were apparent regarding visual obstruction reading (VOR), an index of plant biomass, and litter depth. VOR changed little over the growing season in occupied native plots, but it was lower during the drought year (Table 6). In unoccupied native sites, VOR was slightly higher but also changed little over the season (Table 7). However, in crop fields

VOR increased drastically between May-July during the non-drought year (from 0.81 ± 1.56 cm in May to 17.89 ± 1.58 cm in July). This change did not occur during the drought and VOR remained low throughout the season (Table 8). Litter depth was low on occupied native sites (average 1–2 mm) and averaged 2–4 mm on unoccupied native sites in 2020. There was a very slight decrease in litter depth over the season. In crop fields, litter depth was higher in May and the decrease over the season was more pronounced (Tables 6–8).

In summary, occupied native sites included slightly less grass cover, litter cover, and exotic plant cover than unoccupied sites. They also included higher amounts of bare ground, lichen, crust, and spikemoss. Biomass and litter depth were also lower in occupied plots. While some of these differences were marginal, this is what we should expect for a short-grass specialist in this region. We detected notable differences in vegetation conditions between years resulting from weather variability, but conditions on native sites remained relatively stable across the season. Vegetation conditions changed over the growing season in crop fields, sometimes substantially. Changes in plant cover and biomass were more pronounced in crop fields during the non-drought year. Bare ground was notably higher in crop sites than native, and this remained true across the season for both years. The amount of litter was higher in crop sites than native sites in May but decreased as the season progressed. Interestingly, plant/grass cover was nearly halved in July during the drought year on both crop and native sites compared to estimates from the non-drought year. The most significant change in any variable was the increase in plant biomass in crop fields from May-July during the non-drought year. Therefore, the amount of bare ground, litter, and plant biomass appear to be the most influential habitat features dictating thick-billed longspur presence, but crop fields present a very different landscape with increased variability between years and within a single season compared to more stable native grassland.

In northeast Montana, in addition to management of croplands for thick-billed longspurs, we recommend aiming to create and maintain native grassland that meets the structural and compositional characteristics exemplified by occupied native sites. On less arid grassland sites, disturbances such as fire and grazing are excellent tools that can be used to maintain short-grass prairie. Habitat extent, patchiness, and landscape context should be region specific and require further study. This recommendation is of primary importance for management within core areas of remaining habitat (Sauer, 2020).

Recommendations for Future Research

While our study provides insight into thick-billed longspur use of crop fields in northern Valley County, our recommendations are limited to this region. Managers could benefit by extending research to other regions of thick-billed longspur range within Montana and beyond, as differences in timing of crop growth and farming operations, weather patterns, soil conditions, crop types grown, and surrounding landscape conditions may drastically alter results from a similar study.

A broader demographic analysis investigating adult, juvenile, and post-fledging survival rates would provide additional insight into population-level impacts. Grassland birds are highly sensitive to variation in adult survival (Sedgwick, 2004; Perlut et al., 2008), but the number of young produced, often a function of nest density, is also important (Pulliam et al., 2021). Little is known regarding fledgling and juvenile survival, as these traits are difficult to estimate. Thick-billed longspurs are often double-brooded, but seasonal habitat conditions that vary differentially in crop and native fields can impact frequency of renesting and the number of broods produced in a single season. Therefore, future research should evaluate the relative contribution of each habitat type to overall fecundity (i.e., fledglings per female per season) and how this varies during drought years. If increased variability of habitat conditions in crop fields translates to increased variability in population growth rates in crop fields, we may expect widespread use of crop fields to contribute to population-level declines (Caswell, 1989). While our estimates for nest survival and the number of young fledged per successful nest are similar to those reported in other studies of thick-billed longspur and similar species (Shaffer et al., 2019; Gaudet et al., 2020; Pulliam et al., 2021; Reintsma et al., 2022), additional information is needed on vital rates across life stages (e.g., renesting rates, juvenile survival, adult survival) and bird movements within a single season. Recent advancements in VHF technology (e.g., Motus Wildlife Tracking System) may improve our ability to estimate key vital rates, seasonal fecundity, and longspur movement rates between crop and native sites.

Evaluating stress hormone levels *sensu* Des Brisay (2018) of fledgling, juvenile, and adult longspurs in crop sites could provide additional insight on habitat quality. Body condition at the start of migration often influences survival of adults and juveniles during migration and winter (Merilä and Svensson, 1997; Angelier et al., 2011; Labocha and Hayes, 2012). In Europe, Kuiper et al. (2015) found that cereal fields used by nesting skylarks contained less abundant

food resources, resulting in lower nestling weights. Lower post-fledging survival in crop sites, reduced condition of adults or young, or lower seasonal fecundity in crop sites would provide evidence for reduced habitat quality of crop sites. Likewise, understanding how food resources differ between crop and native sites and how different farming methods impact soil conditions and arthropod abundance may shed more light on thick-billed longspur ecology in cultivated landscapes.

Conclusion

Our results suggest that crop fields may effectively expand nesting opportunities for thick-billed longspurs in a region where native habitat is confined to grassland patches with arid soils. Minor modifications to cultivated land management practices in this region could benefit longspurs, particularly in relation to timing of mechanical operations. Management is more efficient when we can find actions that benefit multiple species and that are effective across multiple systems (Wilson et al., 2005). However, given the unique habitat requirements of thick-billed longspurs and the variability in cropping systems across the Northern Great Plains, more research is needed before we can make any “catch-all” recommendations across species or systems. Additionally, management strategies unique to cultivated fields should be designed to preclude deleterious effects on other grassland obligate species (Davis et al., 2020). Given the great weight of evidence that conversion to cropland is detrimental to grassland bird populations, we strongly recommend against any conversion of native prairie to benefit longspurs.

Furthermore, future research should explore management practices that promote dynamic patterns of disturbance, bare ground, and short grass in native prairies, especially in early spring when longspurs select territories (Lipsev and Naugle, 2017). This would be particularly important if longspurs require proximal native habitat to select crop fields at a higher order or if variability in crop habitat quality instigates movement of longspurs between nesting attempts. Climate change may exacerbate drought conditions during certain years and is likely to increase overall variability in weather patterns. How this may impact birds nesting in crop fields is a worthwhile avenue for future research. Further investigation into population demographics, body condition, and resource availability may provide additional insight into the suitability of crop fields as nesting habitat. It appears that thick-billed longspurs may be taking advantage of novel niche space in a drastically altered landscape, providing unconventional opportunities for research and management of a unique species in the Anthropocene.

TABLES

Table 1. Derived estimates of mean site-level abundance of thick-billed longspurs in crop and native sites in Valley County, Montana, 2020 and 2021^a. Shown are drought conditions, estimates for May and July, and associated 95% confidence intervals for each estimate. Survey rounds were evenly spaced between 10 May – 15 July each year.

Site Type	Conditions (Year)	Abundance	95% CI	Abundance	95% CI
		May		July	
Crop	Non-drought (2020)	16.8	15.7–18.0	6.5	5.6–7.8
Crop	Drought (2021)	12.3	11.1–13.3	15.1	13.2–17.0
Native	Non-drought (2020)	8.7	7.8–9.7	9.4	8.4–10.7
Native	Drought (2021)	12.7	11.5–14.1	12.1	10.8–13.4

^aSwicegood et al., 2023

Table 2. Apparent causes of nest failure for thick-billed longspurs 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 cause were removed from these calculations.

Cause of Nest Failure	2020		2021	
	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

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

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

Table 3. Estimates of overlapping percent cover from vegetation surveys conducted in native sites occupied by thick-billed longspur in Valley County, Montana, 2020 and 2021^a. Each study plot was surveyed 3 times per year (May, June, July). Because estimates for each variable changed little over the season, only a single combined estimate is reported.

Variable	Conditions	Estimate ±SE (% cover)
Grass	Non-drought	36 ± 6
	Drought	16 ± 4
Residual^b	Non-drought	12 ± 4
	Drought	27 ± 5
Crust^c	Non-drought	21 ± 5
	Drought	18 ± 4
Forb	Non-drought	19 ± 5
	Drought	10 ± 3
Bare Ground	Non-drought	10 ± 4
	Drought	14 ± 4
Spikemoss^d	Non-drought	11 ± 4
	Drought	10 ± 3
Litter^e	Non-drought	8 ± 3
	Drought	11 ± 3
Lichen^f	Non-drought	5 ± 3
	Drought	6 ± 3
Exotic Veg^g	Non-drought	6 ± 3
	Drought	3 ± 2
Rock	Non-drought	4 ± 2
	Drought	4 ± 2
Shrub^h	Non-drought	1 ± 1
	Drought	1 ± 1

^aResults are based on 660 and 840 survey points in native sites in 2020 and 2021, respectively.

^bResidual plant material (grass or forb) that was dead but still standing.

^cAny dried lichen or other non-vegetative material forming a hard surface other than bare ground.

^d*Selaginella* spp.

^eResidual or degraded plant material that was no longer standing.

^fTypically vagrant lichen of genus *Xanthoparmelia*.

^gAny non-native plant species (grass or forb).

^hAny plant with a woody stem; also included all cactus species.

Table 4. Estimates of overlapping percent cover from vegetation surveys conducted in native sites unoccupied by thick-billed longspur in Valley County, Montana, 2020^a. Each study plot was surveyed 3 times (May, June, July). Because estimates for each variable changed little over the season, only a single combined estimate is reported.

Variable	Conditions	Estimate ±SE (% cover)
Grass	Non-drought	44 ± 9
Residual	Non-drought	16 ± 7
Crust	Non-drought	16 ± 7
Forb	Non-drought	17 ± 7
Bare Ground	Non-drought	4 ± 4
Spikemoss	Non-drought	7 ± 5
Litter	Non-drought	21 ± 8
Lichen	Non-drought	1 ± 2
Exotic Veg	Non-drought	11 ± 6
Rock	Non-drought	1 ± 2
Shrub	Non-drought	0.5 ± 1

^aResults are based on 300 survey points in unoccupied native sites in 2020.

Table 5. Estimates of overlapping percent cover from vegetation surveys conducted in crop sites occupied by thick-billed longspur in Valley County, Montana, 2020 and 2021^a. Each study plot was surveyed 3 times per year (May, June, July). For estimates that changed significantly over the season, multiple estimates are reported. For estimates that remained similar across all three survey rounds, only a single combined estimate is reported.

Variable	Conditions	May	June	July
		Estimate ±SE (% cover)	Estimate ±SE (% cover)	Estimate ±SE (% cover)
Plant Cover^b	Non-drought	4 ± 4	19 ± 8	46 ± 10
	Drought	5 ± 4	19 ± 8	22 ± 8
Residual	Non-drought	8 ± 3	-	-
	Drought	13 ± 4	-	-
Bare Ground	Non-drought	45 ± 6	-	-
	Drought	42 ± 6	-	-
Litter	Non-drought	36 ± 8	20 ± 6	20 ± 6
	Drought	37 ± 8	21 ± 6	20 ± 6
Rock	Non-drought	5 ± 2	-	-
	Drought	5 ± 2	-	-

^aResults are based on 225 and 243 survey points in crop sites in 2020 and 2021, respectively.

^bBecause monoculture plantings typically resulted in one dominant crop species, we ignored classification of plants into grass and forb categories and only quantified overall plant cover in crop fields.

Table 6. Estimates of visual obstruction reading (VOR) and litter depth from vegetation surveys conducted in native sites occupied by thick-billed longspur in Valley County, Montana, 2020 and 2021^a. Each study plot was surveyed 3 times per year (May, June, July).

Variable	Conditions	May	June	July
		(Estimate ±SE)	(Estimate ±SE)	(Estimate ±SE)
VOR^b (cm)	Non-drought	1.95 ±1.14	2.78 ±1.14	2.62 ±1.13
	Drought	0.68 ±1.12	0.57 ±1.12	0.28 ±1.12
Litter	Non-drought	1.58 ±1.06	1.26 ±1.07	1.05 ±1.06
Depth (mm)	Drought	1.01 ±1.06	0.89 ±1.06	0.91 ±1.06

^aResults are based on 660 and 840 survey points in native sites in 2020 and 2021, respectively.

^bVOR represents an index of plant biomass.

Table 7. Estimates of visual obstruction reading (VOR) and litter depth from vegetation surveys conducted in native sites unoccupied by thick-billed longspur in Valley County, Montana, 2020^a. Each study plot was surveyed 3 times (May, June, July).

Variable	Conditions	May	June	July
		(Estimate ±SE)	(Estimate ±SE)	(Estimate ±SE)
VOR (cm)	Non-drought	3.61 ±1.16	5.07 ±1.16	5.79 ±1.15
Litter	Non-drought	3.77 ±1.22	2.70 ±1.23	2.47 ±1.22
Depth (mm)				

^aResults are based on 300 survey points in unoccupied native sites in 2020.

Table 8. Estimates of overlapping percent cover from vegetation surveys conducted in crop sites occupied by thick-billed longspur in Valley County, Montana, 2020 and 2021^a. Each study plot was surveyed 3 times per year (May, June, July).

Variable	Conditions	May	June	July
		(Estimate ±SE)	(Estimate ±SE)	(Estimate ±SE)
VOR (cm)	Non-drought	0.81 ±1.56	0.93 ±1.56	17.89 ±1.58
	Drought	0.72 ±1.54	0.17 ±1.56	1.47 ±1.54
Litter	Non-drought	4.65 ±1.30	1.74 ±1.30	0.58 ±1.31
Depth (mm)	Drought	2.75 ±1.30	1.41 ±1.30	1.35 ±1.30

^aResults are based on 225 and 243 survey points in crop sites in 2020 and 2021, respectively.

FIGURES

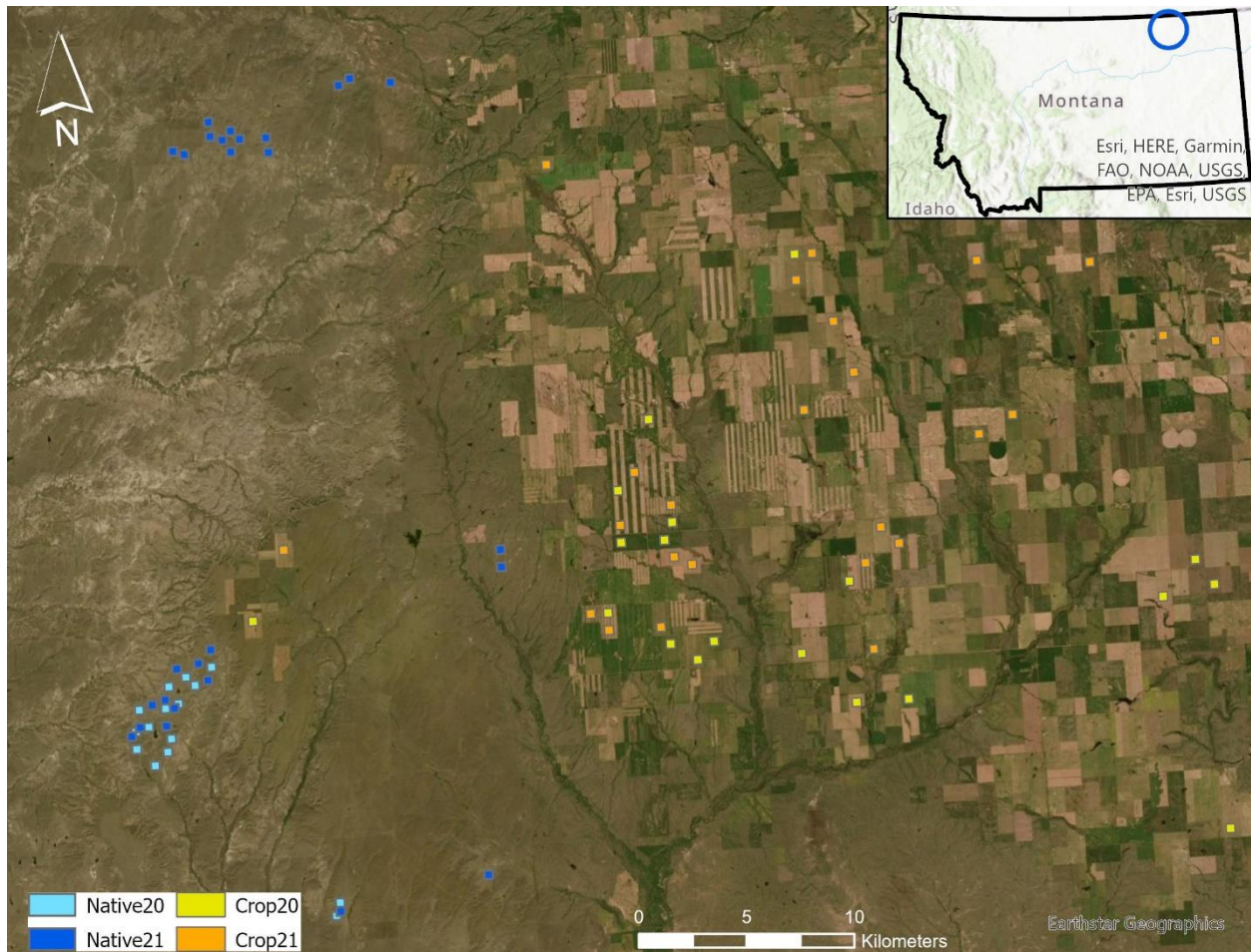


Figure 1. Map of study area and 16-ha plots used for abundance surveys and nest searching on crop and native habitat sites in Valley County, Montana, 2020–21. Clustering of native plots is due to patchy distribution of longspurs in native habitats as these plots were randomly selected from areas known to be occupied by thick-billed longspurs.

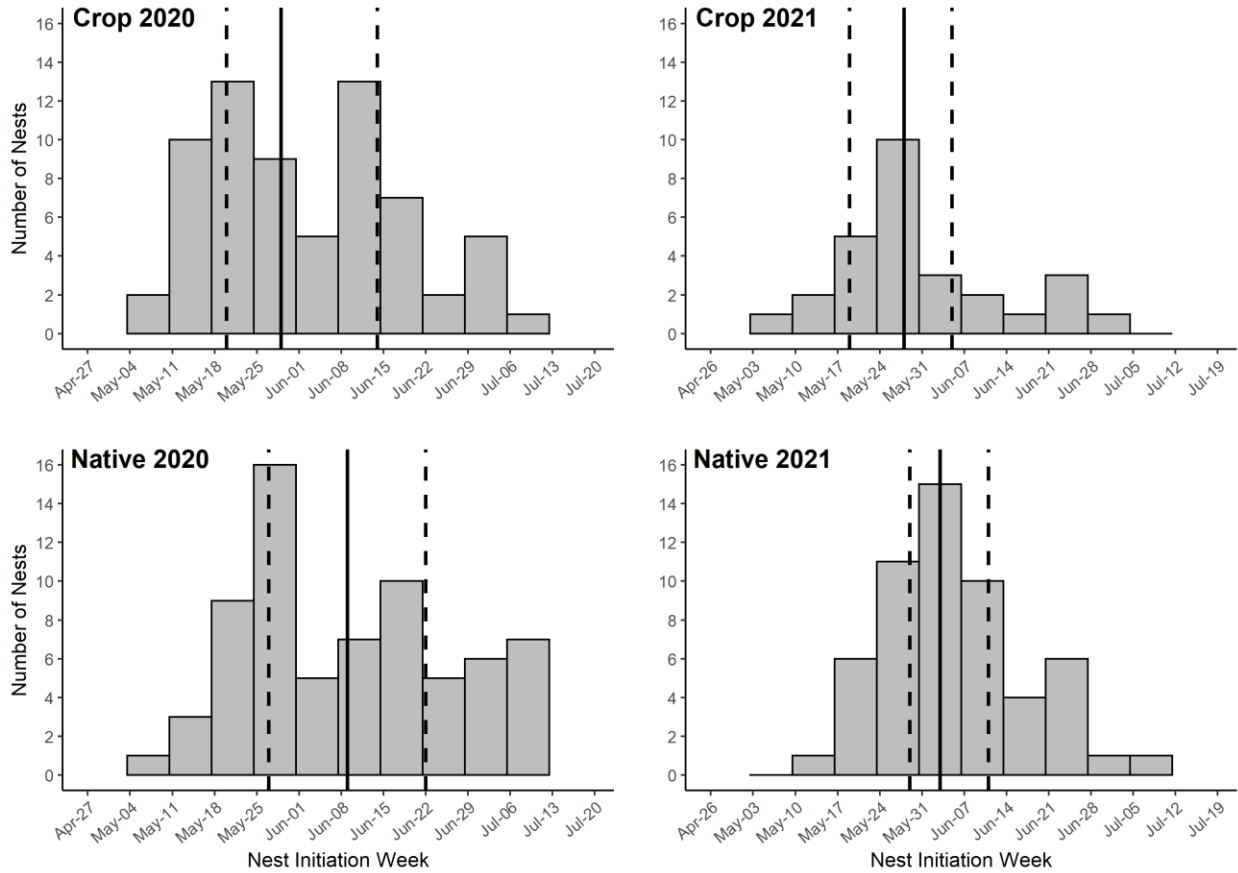


Figure 2. Estimated nest initiation dates in both crop and native sites for 222 thick-billed longspur nests found in Valley County, Montana, 2020–21. Results are based on 139 nests in 2020 (68 crop, 71 native) and 83 nests in 2021 (28 crop, 55 native). Overall nest initiation patterns were similar between crop and native sites given the year; 2020 was relatively cool and wet and 2021 was a drought year. Solid line represents the median nest initiation date and dotted lines represent the first and third quartiles.

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