Breeding-Season Flocking Dynamics of Thick-billed Longspurs (*Rhynchophanes mccownii*) Evidenced by Count Data

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Abstract–Various passerine species are known to shift territories within a single breeding season, including initiating late-season nests in different locations or habitat types. Some migratory birds also exhibit regional movements after nesting but prior to fall migration. Here, we report previously undocumented breeding-season behavior of Thick-billed Longspurs (*Rhynchophanes mccownii*) nesting in crop fields and native grassland habitat in eastern Montana, USA. We observed flocking behavior, resembling pre-migratory staging, during the latter half of the nesting season. These behavioral patterns, revealed through variable spikes in standardized count data, were more prominent in crop sites compared to native grassland sites. We hypothesize that seasonal changes in habitat quality within crop fields may prompt more frequent or erratic movements as longspurs respond to rapidly changing conditions. Further research using tracking or tagging approaches could clarify breeding-season movement patterns and assess potential demographic or population-level consequences associated with such movements.

Introduction

The high mobility of birds facilitates rapid shifts in local abundance across large spatial scales. For passerines, the fitness consequences of some movement types (i.e., seasonal migration and natal dispersal) are well recognized, even if technological limitations hamper our ability to study these movement phenomena (Cox et al. 2014, Faaborg et al. 2010). However, other movement behaviors such as within-season breeding dispersal and post-breeding movements, are less understood (Betts et al. 2008).

Adults of many passerine species are known to disperse to new territories between breeding attempts within a single season (Gow and Stutchbury 2013, Grégoire and Cherry 2007, Powell and Frasch 2000, Williams and Boyle 2019). Within-season breeding dispersal is often attributed to nest failure or competition avoidance, depletion of food resources, or changes in habitat quality, and is presumed to be more common in highly variable or unpredictable habitats (Gow and Stutchbury 2013, McPeek and Holt 1992, Williams and Boyle 2018). Territorial shifts within a breeding season may allow birds to avoid predation or move to higher quality habitats, thereby increasing annual reproductive success (Williams and Boyle 2019). Breeding dispersal may allow species living in variable environments to track changes in habitat suitability over the breeding season (Betts et al. 2008). However, multi-brooded species that experience extreme variability in habitat conditions or nest success from year-to-year may truncate breeding early, particularly during bad weather conditions or when food availability is low (Lv et al. 2020, Walker et al. 2016). Early cessation of nesting attempts can lead to reduced reproductive output during such years (Lv et al. 2020).

Rhynchophanes mccownii Lawrence (Thick-billed Longspur) is a shortgrass specialist and breeding endemic to the northern mixed-grass prairies of North America. Historically, these grasslands were naturally dynamic systems, shaped by interacting patterns of fire,

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grazing, and variable precipitation that created a shifting mosaic of habitat conditions at broad spatial scales (Fuhlendorf et al. 2006, Samson et al. 2004). Thick-billed Longspurs likely depended on large-scale disturbances to maintain patches of shortgrass prairie habitat or short-statured herbaceous vegetation, which they prefer for nesting (Felske 1971, With 2021). In contemporary landscapes, however, little is known about within-season site fidelity or post-breeding movement behavior of this species. Swicegood et al. (2023) documented use of crop fields as nesting habitat by Thick-billed Longspurs in northeastern Montana, USA, and described changes in longspur abundance during the late breeding season in response to precipitation and vegetation conditions in crop fields. Here, we expand on those observations by describing previously unreported late-season flocking behavior observed during systematic abundance surveys.

Methods

Our study was conducted in northern Valley County, Montana, USA (48.70996ºN, -106.37436ºE) during the summers of 2020 and 2021. The region is characterized by expanses of native mixed-grass prairie alongside extensive agricultural lands used for cereal and pulse crop production. The climate is semi-arid, but summer precipitation was below average both years of our study, with greater deficits in 2021. The U.S. Drought Monitor (National Drought Mitigation Center 2026) classified much of the region as moderate drought (D1-D2) during 2020 and severe drought (D2-D3) during 2021 (www.drought.gov). The total amount of precipitation recorded at the Glasgow Weather Forecast Office (USC00243555) between 1 May and 31 July was 18.6 cm in 2020 and 6.8 cm in 2021 (NCEI 2020–21).

As part of a broader study examining breeding season habitat use by Thick-billed Longspurs, we conducted systematic surveys to monitor changes in longspur abundance across the nesting season in crop fields and native grassland habitat. Each year, we conducted line transect surveys 6 times between 10 May and 15 July within 16-ha study plots (see Supplemental File 1, available online at https://eaglehill.us/prnaonline/suppl-files/prna-065-Swicegood-s1.pdf for exact dates).

Observers walked a U-shaped line (800 m) within each survey plot, at a pace of 2–3 km h–1, and recorded perpendicular distance and direction to each longspur detected from 0–100 m. Surveys were conducted from 15 min prior to sunrise until 9:00 AM, and each survey was completed within 30 min. Survey rounds were separated by ≥5 days. Thick-billed Longspurs typically arrive on the breeding grounds in Montana in late April and depart in August or September, with nesting occurring primarily from early May through August (With 2021). Crop fields at the study site included planted cereal and pulse crops, primarily *Triticum aestivum* L. (spring wheat), *Lens culinaris* Medik (lentil), and *Linum usitatissimum* L. (flax) (Swicegood et al. 2023).

We used distance sampling to estimate longspur abundance during each survey round; however, the flocking behavior reported in this note was evident as extreme outlying values (i.e., “spikes”) in plot-level counts, with unusually high numbers of birds observed during certain late-season surveys. As such, the results presented here are based on raw count data rather than model-based abundance estimates. Partial pooling inherent to distance sampling models would draw estimates toward the overall mean and thus dampen the magnitude of these extreme observations. Consequently, derived latent abundances at the plot-level would not fully capture the episodic spikes observed in the field.

To quantify the magnitude of late-season increases in longspur counts, we compared the maximum observed count in each plot during the first 3 survey rounds (mid-May–early June) with the maximum observed count during the last 3 survey rounds (mid-June–mid-July). Counts included all Thick-billed Longspurs observed, although most detections (80%) were of singing males. We did not distinguish sexes in our analysis, and young-of-the-year were almost never detected during transect surveys (<2% of detections) unless they were very close to the transect line. Because detection probability may vary among observers, we focus on pronounced increases in bird counts that were sufficient to overcome observer-related variability, defining notable spikes as those representing at least a three-fold increase relative to early-season maximum counts (Supplementary File 1).

We also searched for and monitored Thick-billed Longspur nests throughout the breeding season to document nesting phenology. Nests were located primarily through behavioral observations of females within each 16-ha plot and were monitored every 2–4 days until fledging or failure. We supplemented behavioral searching with standard rope-dragging methods in some plots and recorded incidental nests found while conducting bird or vegetation surveys. Active nest searching occurred from 9 May–22 July 2020 and from 5 May–8 July 2021 (Swicegood et al. 2023).

Results

We surveyed 24 crop sites and 22 native sites in 2020, and 25 sites of each habitat type in 2021. Raw counts of Thick-billed Longspurs were generally highest during the first survey round (mid-May), appeared to stabilize during rounds 2 and 3 (late May–early June), and showed marked increases on some plots during at least 1 of the final 3 survey rounds (late June–mid-July).

Across the two years, ≥3× increases in raw counts during the second half of the nesting season were more frequently observed in crop sites than in native grassland sites and occurred more often in 2021 than in 2020 (Fig. 1). Between early- and late-season periods, ≥3× spikes in counts occurred in 1 crop plot (4%) in 2020 and 4 crop plots (16%) in 2021. A single ≥3× spike was observed in native grassland sites in 2021 (4%), and none were observed in native sites in 2020. During 2021, 4 crop plots that exhibited ≥3× spikes all reached their maximum counts during the fifth survey round (Fig. 1). In contrast, most crop plots in 2020 recorded 0 longspurs during the final survey round. Table 1 summarizes the frequency of ≥3× spikes by habitat type and year; we also report ≥2× increases, which were notable but below our predefined threshold.

Observers reported the ≥3× spikes as conspicuous events in the field due to the high number of longspurs detected during a single survey. During these surveys, longspurs were abundant throughout the plot and exhibited high level of vocal activity. Singing males comprised approximately 80% of detections during spike events, a proportion similar to that recorded during non-spike surveys. When plots with elevated counts were revisited during subsequent survey rounds, similarly high counts were not observed.

We found and monitored 240 Thick-billed Longspur nests, including 111 nests in crop sites and 129 nests in native grassland sites. Of these, 174 nests were located using behavioral cues, 14 via rope-dragging methods, and 52 incidentally during other field activities. During the 2 years of our study, the earliest nest initiation date was 3 May in both crop and native sites. The latest initiation dates were 6 July (crop) and 16 July (native). Given laying periods of 3–4 days, incubation of approximately 12 days, and nestling periods of roughly 10 days, nesting activity extended through the period in which late-season spikes in counts were observed.

Discussion

The high variability observed in Thick-billed Longspur counts indicates that local abundance within individual survey plots was unlikely to remain constant across the May–July breeding period. High counts during the first survey round likely indicate the presence of late migrants as birds settled onto territories in early May. The late-season spikes in counts gave the impression of transient flocks moving through the area at spatial scales larger than our 16-ha plots, as these temporary count increases exceeded what would be expected from random variation alone. Additionally, the synchrony of the 4 plots that spiked during round 5 in crop sites in 2021 suggests a more coordinated movement pattern of longspurs through crop sites.

Because individuals were unmarked, we cannot determine whether longspurs observed during these spike events were local breeders, immigrants from nearby breeding areas, or birds originating from other habitat types. Likewise, we cannot assess the degree of within-season site fidelity; territorial turnover; or whether these movements involved failed breeders, successful breeders, or birds initiating late nests. However, the episodic timing suggests that longspurs had either completed nesting for the season or were searching for more suitable habitat in which to start a late nest or a renest.

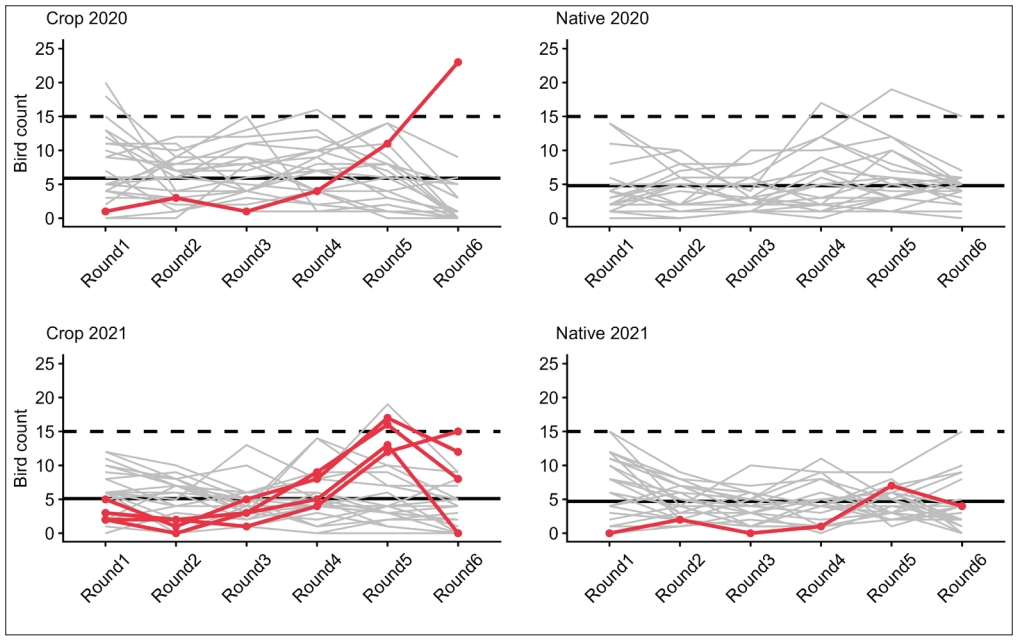


Figure 1. Raw count data plotted over 6 survey rounds (10 May–15 July) for Thick-billed Longspurs within each 16-ha study plot in northern Valley County, Montana, USA. In 2020, 24 study plots were surveyed in crop fields and 22 in native grassland; in 2021, 25 study plots were surveyed in each habitat type. The first column shows counts in crop fields during each study year and the second column shows counts in native grassland habitats. Trend lines of raw counts in each study plot are shown by individual gray lines, with counts from plots that exhibited a ≥3× spike highlighted in red; the solid horizontal line indicates the mean number of longspurs counted over all survey rounds in that habitat type that year, and the dashed horizontal line is drawn at 3× that average.

Adult Thick-billed Longspurs are known to reduce territorial behavior and gather in feeding flocks during the prebasic molt period, which begins in late July on the breeding grounds, with males beginning molt 15–20 d earlier than females (With 2021). However, the spikes in counts documented here occurred primarily in June and early July, preceding the expected onset of molt-related flocking. Thick-billed Longspurs are capable of producing multiple broods in a season, with nest initiation dates in Montana extending into late July (With 2021). During our study, spikes occurred while active nesting was still documented in both crop fields and native grassland, indicating that these late-season movements occurred within the breeding window rather than during a clearly post-breeding period.

Within-season habitat shifts have been documented in other passerines, particularly in species occupying dynamic landscapes. Individuals may move to higher-quality habitat following changes in vegetation structure, resource availability, or breeding success (Betts et al. 2008, Gow and Stutchbury 2013, Williams and Boyle 2019). Crop fields represent highly dynamic environments: They are largely barren when longspurs arrive on the breeding grounds, but vegetation structure can change rapidly as the growing season progresses. Similar to other shortgrass specialists (e.g., *Oenanthe oenanthe* L. [Northern Wheatear]) (Arlt and Pärt 2008), longspurs appeared to shift from tall to short crop vegetation layers in response to changing habitat conditions in crop fields (Swicegood et al. 2023). Such responsiveness to changing conditions implies an ongoing ability to assess and compare

Table 1. Observed spikes in raw counts of Thick-billed Longspurs in Valley County, Montana, USA, during the summers of 2020–2021. Only plots that experienced a ≥2× increase in longspur counts are included, and we consider counts ≥3× able to overcome potential differences in detectability among observers. Observations are divided by year and summarized by habitat types. Plot is the plot identifier. First Max is the maximum bird count during the first half of the breeding season (mid-May to early June). Second Max is the maximum count during the second half (mid-June to mid-July), and the Fold Increase indicates the magnitude of the change.

2020

Plot	Habitat	First Max	Second Max	Fold Increase
crop_66	Crop	3	23	7.7×
native_101	Native	8	17	2.1×

2021

Plot	Habitat	First Max	Second Max	Fold Increase
crop_5	Crop	5	17	3.4×
crop_21	Crop	2	15	7.5×
crop_22	Crop	3	16	5.3×
crop_30	Crop	3	13	4.3×
crop_15	Crop	8	19	2.4×
native_215	Native	2	7	3.5×
native_219	Native	3	8	2.7×

available habitats. Comparable exploratory or assessment-driven movement during the breeding season has been suggested in other grassland passerines, such as the "distant flight behavior" described for *Spiza americana* Gemlin (Dickcissel), which may allow individuals to evaluate alternative breeding opportunities mid-season (Schartz and Zimmerman 1971).

In addition to local habitat tracking, some migratory species make broader regional movements immediately after the breeding season, sometimes forming large flocks prior to the onset of fall migration (Bégin-Marchand et al. 2022; Brown and Taylor 2015, 2017; Vega Rivera et al. 1999). The timing and intensity of such movements may be influenced by weather conditions and interannual variation in habitat quality (Holthuijzen et al. 2022, Renfrew et al. 2020). Although the movements observed in our study occurred earlier than typically expected for post-breeding dispersal, their increased prevalence during a drought year suggests that large-scale environmental conditions could influence the timing or expression of such behavior.

Our study was not designed to track individual movements or quantify demographic consequences, and our observations were limited geographically. Consequently, the biological significance of the observed flocking behavior remains uncertain. Based on the available evidence, we propose two non-mutually exclusive hypotheses: (1) late-season flocking reflects within-season movement by breeding birds attempting to track spatially and temporally variable habitat conditions, particularly in crop fields, and (2) flocks consist of birds that have completed breeding and are initiating early regional movements prior to migration. Although the latter may be less likely given the timing of observations within the nesting window, it cannot be excluded, particularly in years characterized by drought and reduced habitat quality.

Early cessation of breeding efforts and high interannual variability of habitat quality in crop fields compared to relatively stable native grasslands could have significant demographic consequences over long time periods and at large scales. Truncated breeding seasons could lead to lower fecundity and recruitment, and unpredictable resources between years may result in missed breeding opportunities, possibly through increased energetic output devoted to finding acceptable resources. As native grasslands continue to be fragmented and converted to cropland, understanding how grassland specialists respond behaviorally to dynamic and increasingly variable habitats will become ever more important. Studies incorporating individual-based tracking and demographic monitoring would be valuable for clarifying the mechanisms and consequences of breeding-season movements suggested by our observations.

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