

The Effects of Management Practices on Grassland Birds— Thick-billed Longspur (*Rhynchophanes mccownii*)

Chapter Y of

The Effects of Management Practices on Grassland Birds



Professional Paper 1842–Y
Version 1.1, March 2022

U.S. Department of the Interior
U.S. Geological Survey

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By Jill A. Shaffer,¹ Lawrence D. Igl,¹ Douglas H. Johnson,¹ Marriah L. Sondreal,¹
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The Effects of Management Practices on Grassland Birds

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Table

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Conversion Factors

International System of Units to U.S. customary units

Multiply	By	To obtain
Length		
centimeter (cm)	0.3937	inch (in.)
millimeter (mm)	0.03937	inch (in.)
meter (m)	3.281	foot (ft)
kilometer (km)	0.6214	mile (mi)
Area		
hectare (ha)	2.471	acre
square kilometer (km ²)	247.1	acre
hectare (ha)	0.003861	square mile (mi ²)
square kilometer (km ²)	0.3861	square mile (mi ²)
Mass		
kilogram (kg)	2.202	pound (lb)

Temperature in degrees Celsius (°C) may be converted to degrees Fahrenheit (°F) as
 $^{\circ}\text{F} = (1.8 \times ^{\circ}\text{C}) + 32.$

Abbreviations

BBS	Breeding Bird Survey
CV	coefficient of variation
SD	standard deviation
spp.	species (applies to two or more species within the genus)

Acknowledgments

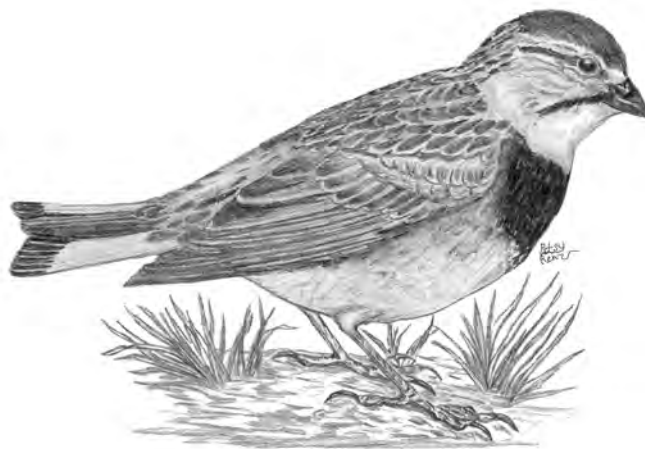
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The Effects of Management Practices on Grassland Birds—Thick-billed Longspur (*Rhynchophanes mccownii*)

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Capsule Statement

The key to Thick-billed Longspur (*Rhynchophanes mccownii*) management is providing short, sparsely vegetated native grasslands of adequate size. Mixed-grass prairies can be made suitable for breeding Thick-billed Longspurs by implementing moderate-to-heavy or season-long grazing. Thick-billed Longspurs have been reported to use habitats with 5–42 centimeters (cm) average vegetation height, 3–7 cm visual obstruction reading, 15–67 percent grass cover, less than (<) 8 percent forb cover, <7 percent shrub cover, 2–60 percent bare ground, 10–63 percent litter cover, and <5 cm litter depth. The descriptions of key vegetation characteristics are provided in table Y1 (after the “References” section). Vernacular and scientific names of plants and animals follow the Integrated Taxonomic Information System (<https://www.itis.gov/>).



Thick-billed Longspur. Illustration by Patsy D. Renz, used with permission.

Breeding Range

Thick-billed Longspurs breed from southern Alberta and southern Saskatchewan; south through Montana, eastern and central Wyoming, and north-central Colorado; and east to western Nebraska, western South Dakota, and southwestern North Dakota (National Geographic Society, 2011). The species also breeds in southeastern Alaska, northern British Columbia, and southwestern Yukon Territory. The relative densities of Thick-billed Longspurs in the United States and southern Canada, based on North American Breeding Bird Survey (BBS) data (Sauer and others, 2014), are shown in figure Y1 (not all geographic places mentioned in report are shown on figure).

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Suitable Habitat

Thick-billed Longspurs use grasslands with sparse litter (Felske, 1971) and low vegetation cover (DuBois, 1935; Creighton, 1974), conditions that are provided by shortgrass prairies or heavily grazed mixed-grass prairies (Saunders, 1914; Finzel, 1964; Wiens, 1970; Maher, 1973, 1974; Creighton, 1974; Oberholser, 1974; Porter and Ryder, 1974; Stewart, 1975; Prescott and Wagner, 1996; McLachlan, 2007; With, 2010; Lipsey, 2015). In southern Saskatchewan, Thick-billed Longspurs were found in equal abundance in tame and native pastures (Davis and others, 1997). Cultivated lands also may be utilized, including small-grain stubble fields, minimum- and conventional-tilled cropland, and summer fallow fields (Felske, 1971; Stewart, 1975; Martin and Forsyth, 2003; McLachlan, 2007), although, historically, agricultural lands were avoided (DuBois, 1935; Mickey, 1943). In a regionwide study encompassing Colorado and Nebraska, Thick-billed Longspurs were significantly more abundant in shortgrass prairies than in dryland agricultural fields, and the species was not observed in Conservation Reserve Program grasslands (McLachlan, 2007).

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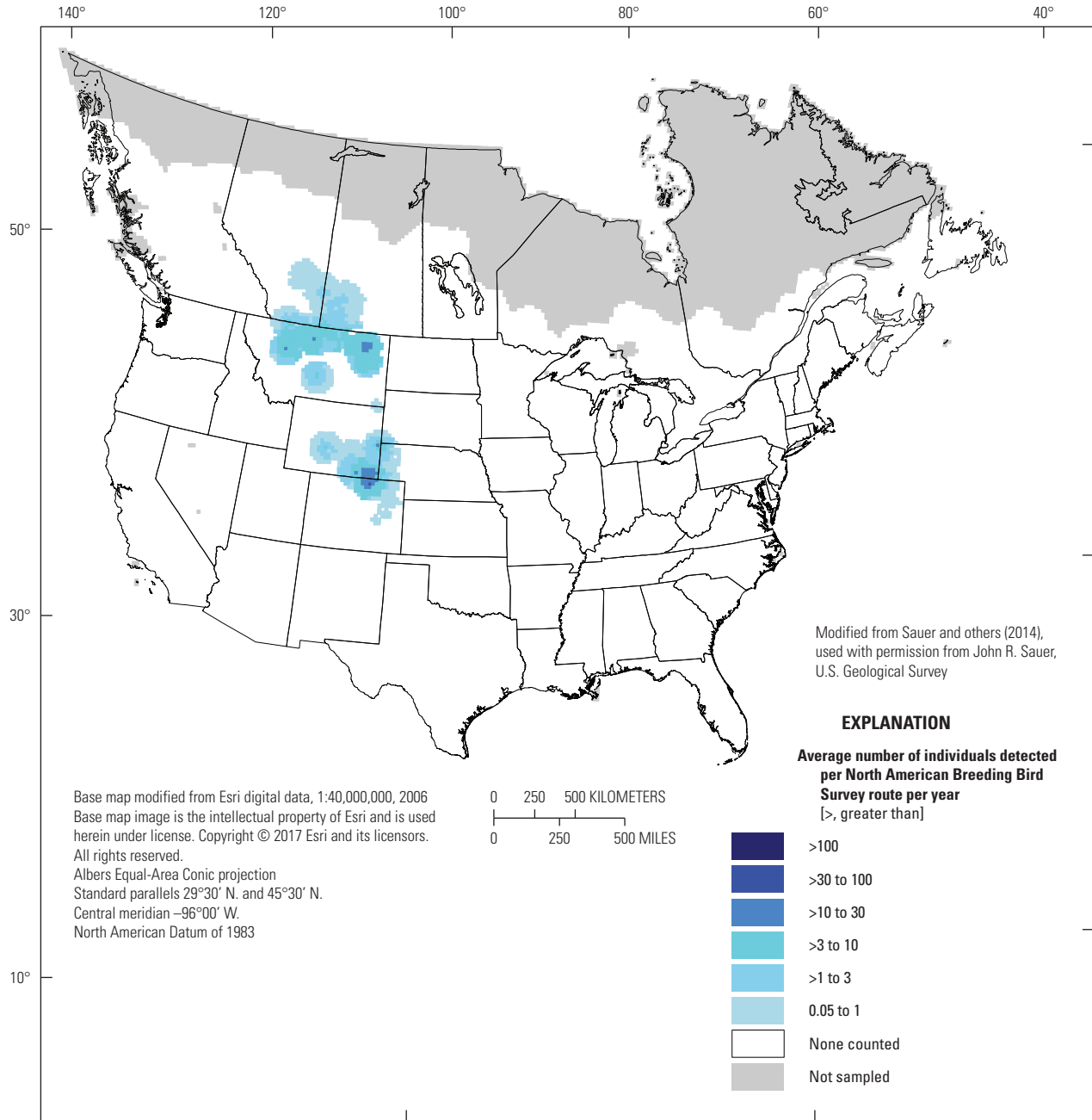


Figure Y1. The breeding distribution of the Thick-billed Longspur (*Rhynchophanes mccownii*) in the United States and southern Canada, based on North American Breeding Bird Survey (BBS) data, 2008–12. The BBS abundance map provides only an approximation of breeding range edges.

Thick-billed Longspur occurrence is affected by vegetation structure. In south-central Alberta, early-season abundance of nesting Thick-billed Longspurs in cropland fields was positively correlated with percentage of bare ground and stubble count (total number of cut plant stems) and negatively correlated with vegetation height (Martin and Forsyth, 2003). In mixed-grass prairies in southwestern Saskatchewan, Thick-billed Longspur occurrence was negatively related to litter and grass coverage (White, 2009). Within those same

Saskatchewan mixed-grass prairies, Bleho (2009) evaluated the relationship between Thick-billed Longspur abundance and vegetation structure at the plot and pasture levels; plots were circular areas of 100-meter (m) radii located within pastures that were grazed season-long (June to October) at moderate grazing intensity (about 43 percent utilization). Two measures of vegetation patchiness (that is, heterogeneity)—standard deviation (SD) and coefficient of variation (CV)—were evaluated. At the plot level, Thick-billed Longspur abundance was

positively associated with vegetation height-density; percentage cover of grass, shrubs, and exposed moss and lichens; the SD-derived measure for patchiness of exposed moss and lichen coverage; and the CV-derived measure for patchiness of vegetation height-density, exposed moss and lichen coverage, and forb coverage. At the pasture level, Thick-billed Longspur abundance was positively associated with the SD- and CV-derived measures for patchiness of shrub coverage. In another study in mixed-grass prairies of southwestern Saskatchewan, Thick-billed Longspur abundance was greatest in areas with tall, sparse grass cover and litter <0.5 cm deep (Kalyn Bogard and Davis, 2014). Henderson and Davis (2014) reported in a fourth southwestern Saskatchewan study that Thick-billed Longspur probability of occurrence decreased as litter mass (in kilograms per hectare) and vegetation height-density increased; abundance decreased as litter mass, vegetation height-density, and shrub cover increased, but increased as bare ground cover increased. The best vegetation model explaining the occurrence of Thick-billed Longspurs in short-grass prairies in Colorado and Nebraska incorporated grass height but not shrub cover; mean occurrence of Thick-billed Longspurs was highest in fields in which <25 percent of the grass was taller than 15 cm (McLachlan, 2007).

Thick-billed Longspurs often breed on high, barren hillsides with southern exposures (Giezentanner, 1970a, 1970b; Felske, 1971; Creighton, 1974). Blue grama (*Bouteloua gracilis*) and buffalograss (*Bouteloua dactyloides*) are dominant plants in nesting areas (DuBois, 1935; Cassel, 1952; Creighton, 1974). Thick-billed Longspur nests tend to be oriented to the north (With and Webb, 1993), and about one-third to one-half of nests are placed near clumps of grass, shrubs, plains pricklypear (*Opuntia polyacantha*), or cow dung (DuBois, 1935; Mickey, 1943; Greer, 1988; With and Webb, 1993; With, 1994). However, shrubs and pricklypear near the nest may facilitate depredation by providing protective cover to predators; in north-central Colorado, nests placed beside shrubs were 2–3 times more likely to be depredated than nests associated with other types of vegetation (With, 1994). Nests depredated during incubation had six times more shrub cover within 1 m of the nest than did successful nests. Nests were fully exposed to solar radiation at midday and had 45 percent total exposure per day (With and Webb, 1993). High exposure to solar radiation may ameliorate cold stress associated with an early breeding season. Nests constructed later in the season were more likely to be constructed near vegetative cover than those constructed earlier in the season. In southeastern Wyoming, preferential placement of territories on areas with a high percentage of bare ground was attributed to microclimate effects such as early warming and drying of nest sites (Greer, 1988). Percentage of vegetation cover within 5 cm of the ground was higher in occupied territories than in unoccupied territories (Greer, 1988; Greer and Anderson, 1989). Occupied territories also had fewer piles of cow dung, less lichen, and lower forb coverage than unoccupied areas.

Seasonal moisture levels may affect the occurrence of Thick-billed Longspurs. In an assessment of BBS data for

the conterminous United States, O'Connor and others (1999) reported a negative relationship between Thick-billed Longspur abundance and mean annual precipitation. In the short-grass steppes of Colorado, Conrey and others (2016) examined the influence of heat, drought, and precipitation on the likelihood of bird species fledging at least one young. Thick-billed Longspur was included with Horned Lark (*Eremophila alpestris*) in the guild of species nesting in the shortest vegetation. The authors concluded that the likelihood for a nest surviving to fledge at least one young was reduced under conditions of drought (periods when at least 10 consecutive days had passed with less than or equal to 1 millimeter [mm] total rainfall), high summer temperatures (greater than or equal to 35 degrees Celsius [°C]), and storm events (days with rain events greater than or equal to 10 mm). Scenarios in which summer temperature increased by 3 °C and seasonal precipitation decreased by 2 additional dry days caused nest success to be halved compared to its current average value. Lipsey (2015) suggested that low-productivity grasslands (that is, those with <1,121 kilograms [kg] per hectare [ha] normal year biomass production) may act as refugia in wet years for species, such as for Thick-billed Longspur, that require sparse vegetation.

Area Requirements and Landscape Associations

Territory size of Thick-billed Longspurs varies by region. Reported territory sizes were 0.5–1 ha in Saskatchewan (Felske, 1971), 0.6 ha in southeastern Wyoming (Greer, 1988; Greer and Anderson, 1989), and 1–1.5 ha in central Colorado (Wiens, 1970, 1971; With, 2010). In southeastern Wyoming, an increase in density of breeding pairs between years did not cause territory size to decrease (Greer, 1988), suggesting that the habitat was not saturated the first year. Pairs often nest near each other (Mickey, 1943; Felske, 1971; Golding and Dreitz, 2017).

For Thick-billed Longspur, no studies have investigated a relationship between patch size and nest success or patch size and rate of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*). Thick-billed Longspurs may be affected by the composition of the surrounding landscape. In the dry mixed-grass prairie region and northern fescue grassland region in southeastern Alberta, Thick-billed Longspur occurrence was negatively related to the percentage of surface water (that is, wetlands, riparian areas, and other watercourses) within a 400-m radius of point-count center (Clements, 2014). In mixed-grass prairies in northeastern Montana, Lipsey (2015) evaluated grassland bird distribution and abundance at four spatial extents (0.7, 2.6, 93, and 1,492 square kilometers [km²]). Thick-billed Longspur densities were lower in landscapes composed of a low percentage of grassland than in landscapes with large and intact grasslands, despite favorable local conditions based on measurements of vegetation cover and structure. Lipsey (2015) estimated that a grassland

of 40,469 ha embedded in a landscape composed of 40 percent grass would support 3,500 Thick-billed Longspurs, whereas the same area embedded in a landscape composed of 15 percent grass would only support 400 Thick-billed Longspurs. In Colorado and Nebraska, McLachlan (2007) reported a negative relationship between Thick-billed Longspur occurrence and the number of land-cover patches and the amount of agricultural land within 300, 600, 1,200, and 2,400 m of point counts, as well as between the amount of barren land within 1,200 and 2,400 m of point counts.

Brood Parasitism by Cowbirds and other Species

The status of Thick-billed Longspur as a host of the Brown-headed Cowbird is not well known (Friedmann, 1963; Maher, 1973). Few records of cowbird brood parasitism have been reported for the Thick-billed Longspur (Shaffer and others, 2019).

Breeding-Season Phenology and Site Fidelity

The Thick-billed Longspur breeding season begins about mid-March (Mickey, 1943; Giezentanner and Ryder, 1969; Felske, 1971; Creighton, 1974; Salt and Salt, 1976; Greer, 1988; With, 2010). Thick-billed Longspurs exhibit low site fidelity (With, 2010). Second broods were reported in Montana, south-eastern Wyoming, and north-central Colorado (DuBois, 1935; Strong, 1971; Greer, 1988). Second broods may be initiated as soon as 3 weeks after fledging of the initial brood but may be limited by female energy reserves (Felske, 1971; With, 2010). Thick-billed Longspurs depart the breeding grounds between October and mid-November (Mickey, 1943; Giezentanner and Ryder, 1969; Felske, 1971; Creighton, 1974; Salt and Salt, 1976; Johnsgard, 1980; Greer, 1988; With, 2010).

Species' Response to Management

Little is known about the short- or long-term effects of prescribed burning of grassland habitat on Thick-billed Longspur populations. Some authors have suggested that prairie fire suppression has contributed to the population decline of the species (Krause, 1968; Oberholser, 1974; With, 2010). White (2009) examined the effect of burning and grazing on the abundance of Thick-billed Longspurs in Saskatchewan mixed-grass prairies; abundance was not influenced by the management treatments. Richardson (2012), who continued the work of White (2009), also reported no consistent influence of burning on the abundance of Thick-billed Longspurs, perhaps

owing to low sample sizes, but determined that Thick-billed Longspurs were most abundant in grazed plots and showed a preference for heavily disturbed sites over ungrazed-unburned sites (see also Richardson and others, 2014). In a study evaluating patch-burn management (that is, applying prescribed burns in a spatially and temporally variable mosaic and allowing large herbivores to select among burned and unburned patches in the landscape) in shortgrass steppe in Colorado, Thick-billed Longspur abundance was unaffected by recent (2-, 3-, and 4-year-old) burns, although the authors predicted that the species would increase in response to patch burning (Augustine and Derner, 2015).

In areas where grass is too tall or too thick for Thick-billed Longspurs, grazing can improve habitat by providing shorter, sparser vegetation (Giezentanner, 1970a; Stewart, 1975; Kantrud and Kologiski, 1982; Bock and others, 1993; Bleho, 2009). Heavily grazed areas with aridic boroll soils and moderately grazed areas with aridic ustoll soils appeared to be ideal nesting habitat in portions of Montana, North Dakota, Wyoming, Colorado, and Nebraska (Kantrud and Kologiski, 1982). In Alberta, Thick-billed Longspurs preferred season-long grazed native pastures and were fairly common in native pastures grazed in early summer (Prescott and others, 1993; Prescott and Wagner, 1996). Thick-billed Longspurs infrequently occupied spring-grazed (late April to mid-June) pastures of crested wheatgrass (*Agropyron cristatum*), and they avoided deferred-grazed (grazed after July 15) native pastures. In north-central Alberta, Thick-billed Longspurs used moderately to heavily grazed grasslands on drier, sandier sites than those used by Chestnut-collared Longspurs (*Calcarius ornatus*) (Wershler and others, 1991). Thick-billed Longspurs nesting in Alberta and Saskatchewan favored season-long grazed native pastures over areas managed with complementary grazing (early-season grazing on crested wheatgrass with cattle rotated through several native-grassland paddocks for the remainder of the summer) (Dale and McKeating, 1996). Thick-billed Longspurs did not breed on idle mixed-grass pastures in Saskatchewan and preferred heavily grazed pastures over lightly or moderately grazed pastures (Felske, 1971). Bleho (2009), Sliwinski (2011), and Richardson (2012) also evaluated Thick-billed Longspur use of Saskatchewan native pastures. Bleho (2009) reported that Thick-billed Longspurs were more than seven times more abundant in grazed mixed-grass pastures than in ungrazed pastures. Sliwinski (2011) reported that Thick-billed Longspurs preferred mixed-grass prairies that were heavily grazed by American bison (*Bison bison*). In northeastern Montana, Thick-billed Longspur preferred low-productivity grasslands with poor soils and occurred more frequently in low-productivity grasslands than expected based on habitat area (Lipsey, 2015). Lipsey (2015) indicated that grazing intensity did not measurably affect abundance of Thick-billed Longspur, which may reflect that this species was seldom observed during the study. In central Montana grasslands dominated by Wyoming big sagebrush (*Artemisia tridentata* species [spp.] *wyomingensis*) and intermixed with western wheatgrass (*Pascopyrum smithii*), needle and thread (*Hesperostipa comata*),

blue grama, and junegrass (*Koeleria macrantha*), Golding and Dreitz (2017) reported that Thick-billed Longspurs were more than twice as abundant (33–36 birds per 25 ha compared to 13–14 birds per 25 ha, respectively) in areas with rest-rotation grazing (that is, alternating 2–3-month grazing periods, followed by 15–18 months of rest) than in areas with season-long grazing (that is, continuous grazing during growing season). In Colorado shortgrass prairies, summer-grazed areas were preferred over winter-grazed areas (Giezentanner and Ryder, 1969; Giezentanner, 1970a, 1970b; Wiens, 1970). Overgrazing may be detrimental to grasslands (Oberholser, 1974), particularly in arid, sparse shortgrass prairies (Ryder, 1980).

Use of cultivated lands has included small-grain stubble fields, minimum- and conventional-tilled land, and summer fallow fields (Felske, 1971; Stewart, 1975; Martin and Forsyth, 2003). In Alberta and Saskatchewan, Thick-billed Longspurs were more abundant in cropland than in Permanent Cover Program grasslands (McMaster and Davis, 1998). In Alberta cropland, productivity scores (an index of reproductive behavior) were very low in winter wheat (*Triticum* spp.) fields (Martin and Forsyth, 2003). In 1 of 2 years, Thick-billed Longspurs were more productive in minimum-tilled than in conventional-tilled summer fallow fields. In both years combined, productivity was higher and abandoned territories were fewer in minimum-tilled than in conventional-tilled small-grain fields, whereas abandoned territories were greater in minimum-tilled than in conventional-tilled summer fallow fields (Martin and Forsyth, 2003). In recent years, several studies have evaluated the use of reproductive indices, such as the one used by Martin and Forsyth (2003), as an alternative to nest searching and monitoring of grassland birds and suggested that reproductive indices often lack the ability to predict nest fate or to provide reliable estimates of reproductive performance at the territory or plot level (Rivers and others, 2003; Althoff and others, 2009; Morgan and others, 2010). The results related to productivity reported by Martin and Forsyth (2003) should be evaluated within the context and caveats of the growing body of literature on this topic.

Some pesticides may have deleterious effects on Thick-billed Longspurs. At the Pawnee National Grassland in Colorado, malathion and toxaphene were applied at rates of 0.6 and 1.1 kg per ha, respectively (McEwen and Ells, 1975). Densities of Thick-billed Longspurs were higher in grasslands treated with malathion or toxaphene than in untreated grasslands; however, nestlings were killed by toxaphene.

Thick-billed Longspur abundance and productivity may be lower near energy-generating infrastructure. In southwestern Saskatchewan, abundance of Thick-billed Longspurs increased with distance from gas wells, with higher abundances occurring beyond 600 m from wells (Kalyn Bogard, 2011; Kalyn Bogard and Davis, 2014). However, abundance was greater in legal sections (259 ha) with at least one gas well relative to legal sections without wells. In Alberta, Linnen (2008) reported that Thick-billed Longspur abundance decreased near oil wells and access roads, and the species exhibited an avoidance of areas within 300 m of

oil development, although not significantly so. In Wyoming, Mahoney and Chalfoun (2016) evaluated the effect of wind facilities on Thick-billed Longspur reproductive success. Measures of reproductive success, including clutch size, number of fledglings, size-adjusted nestling mass, and daily nest survival, did not differ between undeveloped reference sites and wind-facility sites. Nest-survival rates were negatively related to turbine density within 1 kilometer of nests, vegetation density at 10–20 cm height, and grassland area within the neighborhood of a nest. Nest survival decreased with increasing vegetation density when considered together with turbine density and the amount of grassland habitat in the neighborhood of the nest. Habitat and distance to infrastructure did not explain clutch size, number of fledglings, or size-adjusted nestling mass (Mahoney and Chalfoun, 2016). Beston and others (2016) developed a prioritization system to identify avian species most likely to experience population declines in the United States from wind facilities based on the species' current conservation status and the species' expected risk from wind turbines. At a score of 4.29, the Thick-billed Longspur was among 40 species (of 428 species evaluated) with an average priority score of at least a four or above out of nine. Beston and others (2016) estimated that 7.02 percent of the Thick-billed Longspur breeding population in the United States is exposed to wind facilities.

Management Recommendations from the Literature

Providing grassland areas of adequate size may help to support multiple Thick-billed Longspur territories, as pairs often nest near each other (Mickey, 1943; Wiens, 1970; Felske, 1971; Greer, 1988; Greer and Anderson, 1989; With, 2010). Thick-billed Longspur habitat should be protected from agricultural and urban development (Oberholser, 1974; McLachlan, 2007; With, 2010).

Areas with little litter and short, sparse vegetation with low coverage of forbs are important for Thick-billed Longspurs (DuBois, 1935; Felske, 1971; Maher, 1973, 1974; Stewart, 1975; McLachlan, 2007; With, 2010). Prescribed prairie burns have been recommended for areas where fires occurred historically but now have been suppressed (Krause, 1968; Oberholser, 1974; With, 1994; Richardson, 2012). Vegetation that is already sparse and short from grazing, especially in areas of low precipitation, should not be overgrazed (Oberholser, 1974; Ryder, 1980). Grasslands with vegetation that is too tall or dense for nesting by Thick-billed Longspurs may be grazed to encourage longspur use (Giezentanner, 1970a, 1970b; Felske, 1971; Stewart, 1975; Kantrud and Kologiski, 1982; Bleho, 2009; Richardson, 2012; Richardson and others, 2014). Based on findings by Kalyn Bogard and Davis (2014) in grazed mixed-grass prairies in which the effects of natural gas well proximity and density on grassland songbird abundance varied strongly among species and between regions,

the authors recommended timely cattle rotation, fencing off of gas wells, and allowing adequate resting periods for vegetative regrowth as possible management actions to reduce interactive effects of natural gas development, livestock grazing, and concomitant changes in vegetation structure. Kalyn Bogard and Davis (2014) further recommended that clear management objectives be tailored to the habitat requirements of individual species, as actions taken for one species might have a deleterious effect on another species. In sagebrush ecosystems, Golding and Dreitz (2017) indicated that although a single grazing system (such as rest-rotation grazing) can be used to increase the abundance of an individual songbird species such as the Thick-billed Longspur, a mosaic of numerous grazing systems might better maintain ecological functions and the abundance and distribution of the entire songbird community.

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Table Y1. Measured values of vegetation structure and composition in Thick-billed Longspur (*Rhynchophanes mccownii*) breeding habitat by study. The parenthetical descriptors following authorship and year in the “Study” column indicate that the vegetation measurements were taken in locations or under conditions specified in the descriptor; no descriptor implies that measurements were taken within the general study area.

[cm, centimeter; %, percent; --, no data; >, greater than]

Study	State or province	Habitat	Management practice or treatment	Vegetation height (cm)	Vegetation height-density (cm)	Grass cover (%)	Forb cover (%)	Shrub cover (%)	Bare ground cover (%)	Litter cover (%)	Litter depth (cm)
Bleho, 2009	Saskatchewan	Mixed-grass prairie	Ungrazed	--	7.4 ^a	15.6	4.5	6.2	4.7	60.9	--
Bleho, 2009	Saskatchewan	Mixed-grass prairie	Cattle-grazed	--	4 ^a	17.9	6.9	3.6	8.4	45.2	--
Creighton, 1974	Colorado	Mixed-grass prairie	Grazed	5.2	--	67	2	0.9	23	--	--
Greer, 1988 ^b (territories)	Wyoming	Mixed-grass prairie	Grazed	--	--	50	7.4	6.7	38.1	14.8	--
Kalyn Bogard, 2011	Saskatchewan	Mixed-grass prairie	Grazed	9.5	--	30.8	7.9	--	59.9	--	--
Sliwinski, 2011	Saskatchewan	Mixed-grass prairie	Bison-grazed	27.4	--	28.2	4.8	--	--	--	2.9
White, 2009	Saskatchewan	Mixed-grass prairie	Unburned, ungrazed	41.7 ^c	7.2 ^a	14.8	5.1	2.1	1.6	62.8	5.1
White, 2009	Saskatchewan	Mixed-grass prairie	Unburned, cattle-grazed	41.4 ^c	3.4 ^a	17.3	7.8	0.4	3.2	47.3	2.1
White, 2009	Saskatchewan	Mixed-grass prairie	Burned, ungrazed	39.4 ^c	4 ^a	31.4	6.8	0.5	15.4	10.4	1.1
White, 2009	Saskatchewan	Mixed-grass prairie	Burned, cattle-grazed	37.2 ^c	3.5 ^a	30.7	6.1	0.7	19.5	14.9	1.6
Wiens, 1970 ^d (territories)	Colorado	Shortgrass prairie	Heavy summer-grazing intensity	--	0.4 ^c	78.5	0	0	19	16.8	0.18

^aVisual obstruction reading (Robel and others, 1970).

^bThe sum of the percentages is >100%, based on methods described by the author.

^cMaximum vegetation height.

^dThe sum of the percentages is >100%, based on the modified point-quadrat technique of Wiens (1969).

^eEffective vegetation height.

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