

Co-occurrence and nest success of Thick-billed and Chestnut-collared Longspurs in a central Montana rangeland

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ABSTRACT.—Thick-billed and Chestnut-collared Longspurs (*Rhynchophanes mccownii* and *Calcarius ornatus*, respectively) are 2 grassland bird species that are indicative of the widespread decline of grassland passerines in North America. In our central Montana study area, we observed these 2 species nesting within close proximity (<40 m apart), suggesting that this study area may hold conservation value due to its capacity to support breeding individuals of both species. Given their declining populations and our limited knowledge of their nesting ecology, our objective was to examine the nest success and interspecies nest distances of Thick-billed and Chestnut-collared Longspurs in a central Montana rangeland. We conducted systematic and opportunistic nest searches from 2013 to 2019 to determine nest fate and nest locations. We found a total of 259 Thick-billed Longspur nests and 34 Chestnut-collared Longspur nests. Incubation survival rates were 0.45–0.61 for Thick-billed Longspurs and 0.50–0.81 for Chestnut-collared Longspurs. Nestling survival rates were generally higher than incubation rates, ranging from 0.39 to 0.88 for Thick-billed Longspurs and 0.72 to 0.90 for Chestnut-collared Longspurs. The estimated survival rate for incubation and nestling stages combined was 0.19–0.43 for Thick-billed Longspurs and 0.36–0.73 for Chestnut-collared Longspurs. Chestnut-collared Longspur nests were frequently found in the same pasture as Thick-billed Longspur nests, with a total of 28 Chestnut-collared Longspur nests sharing pastures with 62 Thick-billed Longspur nests. The mean distance between Chestnut-collared Longspur nests and the nearest Thick-billed Longspur nest was 370 m (SE = 95 m) and ranged from 32 to 2230 m. Our work provides additional insights into the nesting ecology of these declining grassland songbird species by identifying a region that can support successful reproduction for both Thick-billed and Chestnut-collared Longspurs.

RESUMEN.—El escribano de pico grueso (*Rhynchophanes mccownii*) y el escribano de collar castaño (*Calcarius ornatus*) son dos especies de aves de pastizales indicadoras de la disminución generalizada de los passeriformes de pastizales en América del Norte. En nuestra área de estudio en el centro de Montana, observamos a estas dos especies anidando muy cerca (<40 m), lo que sugiere la importancia de conservar esta área de estudio por su capacidad de sustentar individuos reproductores de ambas especies. Dado que sus poblaciones han disminuido y el conocimiento acerca de su ecología de anidación es limitado, nuestro objetivo fue examinar el éxito de anidación y la distancia de los nidos inter-especie de los escribanos de pico grueso y de collar castaño en un pastizal en el centro de Montana. Entre 2013 y 2019, llevamos a cabo búsquedas sistemáticas y oportunistas de nidos para determinar su destino y ubicación. Encontramos un total de 259 nidos de escribanos de pico grueso y 34 nidos de escribanos de collar castaño. La tasa de supervivencia de incubación fue de 0.45 a 0.61 en los escribanos de pico grueso y de 0.50 a 0.81 en los escribanos de cuello castaño. La tasa de supervivencia de los polluelos fue generalmente más alta que la tasa de incubación, oscilando entre 0.39 y 0.88 en los escribanos de pico grueso y 0.72 a 0.90 en los escribanos de collar castaño. La tasa de supervivencia estimada para las etapas de incubación y de anidación combinadas fue de 0.19 a 0.43 en los escribanos de pico grueso y de 0.36 a 0.73 en los de collar castaño. Los nidos de los escribanos de pico grueso se encontraron con frecuencia en el mismo pasto que los nidos de los escribanos de pico grueso, con un total de 28 nidos de escribanos de collar castaño que compartían pastos con 62 nidos de escribanos de pico grueso. La distancia promedio entre los nidos de los escribanos de cuello castaño y de pico grueso fue de 370 m (ES = 95 m) y osciló entre 32 m a 2230 m. Nuestro trabajo proporciona información adicional sobre la ecología de anidación de estas especies de aves cantoras de pastizales en declive al identificar una región que podría sustentar una reproducción exitosa tanto de escribanos de pico grueso como de escribanos de collar castaño.

Grassland birds are the fastest declining avian guild in North America (Rosenberg et al. 2019). Thick-billed Longspurs (*Rhynchophanes mccownii*) and Chestnut-collared Longspurs

(*Calcarius ornatus*) are 2 sympatric grassland-obligate species experiencing precipitous population declines. Long-term population trends (1966–2015) indicate a 94% decline for Thick-billed

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Longspurs and an 87% decline for Chestnut-collared Longspurs across their ranges (Sauer et al. 2017). As a result, both species have been designated as species of high conservation concern in both the United States and Canada (Somershoe 2018). These population declines are attributed to widespread grassland habitat loss and degradation, largely due to agricultural conversion (Lark et al. 2015). Energy extraction infrastructure (e.g., wind, oil, and natural gas) further encroaches on remaining grassland habitat and negatively impacts demographic rates (Mahoney and Chalfoun 2016, Ng et al. 2019). These landscape changes may increase nest predation and brood parasitism rates (Tewksbury et al. 2006, Vander Haegen 2007, Bernath-Plaisted et al. 2017), resulting in reduced reproductive success (Davis 2003).

Thick-billed and Chestnut-collared Longspur conservation hinges on identifying habitat conditions conducive to successful reproduction. Overlapping breeding ranges between Thick-billed and Chestnut-collared Longspurs indicate that these species likely select for similar habitat characteristics at broad scales (Veech 2006). Both species occur within short- and mixed-grass prairies and select for lower herbaceous cover than other grassland passerines (Augustine and Baker 2013, Henderson and Davis 2014, Lipsey and Naugle 2017, With 2021). However, the co-occurrence of these species at finer scales may be uncommon due to different nesting preferences (Sedgwick 2004a, 2004b, With 2021). For instance, Thick-billed Longspurs are associated with relatively barren sites with short grasses and bare ground (Conrey et al. 2016). In short-grass prairie, they select nest sites with approximately 2.5 to 3 cm of visual obstruction (Skagen et al. 2018). In contrast, Chestnut-collared Longspurs prefer areas with taller and denser vegetation (Augustine and Baker 2013, Lipsey and Naugle 2017, Pulliam et al. 2020) where nest sites have an average vegetation height of approximately 16 cm in mixed-grass prairie (Davis 2005).

Here, we report on the nest success and co-occurrence of nesting Thick-billed and Chestnut-collared Longspurs in central Montana. Our observations of these 2 species nesting in close proximity (<40 m apart) are notable given their different fine-scale nesting preferences (Lipsey and Naugle 2017, Pulliam et al. 2020, With 2021). The sympatric nesting we documented may indicate that this study area is of conservation

value due to its capacity to support species with divergent fine-scale nesting preferences. Given ongoing habitat loss (Lark et al. 2015, Mahony et al. 2022), targeting conservation efforts in habitats that support breeding individuals of both species could maximize conservation efforts for resource-limited agencies.

As part of a larger study examining songbird diversity and demographics, we established 94 plots of 500 × 500 m that were randomly placed within 89,000 ha of private and public land near Roundup, Montana (46.4452°N, 108.5418°W, 980 m elevation; Golding and Dreitz 2017). Pastures containing plots ranged in size from 0.6 to 14.8 km² (\bar{x} = 4.1 km², SD = 0.2 km², n = 59), though there were some pastures that we did not have spatial data for. Sagebrush shrubs (*Artemisia tridentata* ssp. *wyomingensis*) and grasses (i.e., needle and thread [*Hesperostipa comata*] and western wheatgrass [*Pascopyrum smithii*]) were the dominant vegetation. From 2013 to 2019, we conducted systematic nest searching by dragging a 10-m chain between 2 observers where the chain was centered on an established transect line. Following Reintsma et al. (2022), transect lines were distributed evenly in the plot with 100-m spacing. Opportunistic nest searches occurred whenever observers were in the plots for other study activities aside from nest searches (i.e., nest monitoring). We did not perform nest searches during extreme temperatures (e.g., below freezing) or precipitation.

For each nest located, observers recorded nest GPS locations, photographed the offspring, and marked the nest location using flagging placed 5 m from the nest in the 4 cardinal directions. Nests were monitored every 3 d until they became inactive. We estimated nestling age using developmental markers, such as eye opening by day 3, egg tooth absence by day 5, and unsheathing pin feathers by day 6 (Mickey 1943, Jongsomjit et al. 2007). Incubation lasts ~12 days for Thick-billed Longspurs and ~11 days for Chestnut-collared Longspurs. The nestling stage (i.e., from hatch date to fledging) is ~10 days for Thick-billed Longspurs and ~11 days for Chestnut-collared Longspurs (Mickey 1943, Jongsomjit et al. 2007, With 2021). Clutch completion dates were assigned between consecutive nest visits when clutch size reached maximum size, or 12 days prior to the estimated hatch date for Thick-billed Longspurs and 11 days for Chestnut-collared Longspurs. If a nest was never observed during clutch completion

TABLE 1. Total number of nests, average clutch size, and average productivity (number of fledglings per successful nest) for Chestnut-collared Longspur (CCLO) and Thick-billed Longspur (TBLO) nests near Roundup, Montana, USA.

Species	Year	Total nests	Clutch size			Productivity		
			<i>n</i>	Mean	SE	<i>n</i>	Mean	SE
CCLO	2013	17	12	3.3	0.4	8	3.1	0.3
	2017	15	12	3.6	0.3	11	3.5	0.2
	2018	2	2	4.5	0.5	1	3.00	NA
TBLO	2013	36	27	3.2	0.2	14	2.7	0.2
	2014	48	35	3.6	0.1	28	3.2	0.1
	2015	23	20	3.1	0.2	8	3.3	0.3
	2016	41	37	3.5	0.1	17	3.1	0.2
	2017	54	42	3.5	0.1	32	3.1	0.1
	2018	35	34	3.1	0.2	10	2.8	0.2
	2019	22	17	3.7	0.2	9	4.0	0.2

or the nestling stage, we assigned clutch completion as the initial observation date. Nest fate was either (1) successful, where nests showed evidence for at least one fledgling departing the nest (e.g., fledgling or adult activity near the nest, fecal matter on the edges of the nest), or (2) failed, where nests either showed signs of failure (e.g., carcasses present, nest destroyed) or offspring had inadequate time to fledge.

We calculated separate daily survival rates for incubation (clutch completion to egg hatch) and nestling (egg hatch to fledgling) stages using the Mayfield estimator for each year (Mayfield 1961, 1975). For failed nests, we used the midpoint between the last observed active and first observed inactive dates as the end of the exposure period (Manolis et al. 2000). For successful nests, we used the expected fledge date (calculated based on nestling age) as the end of the exposure period. The exposure period for nests with uncertain fates was terminated on the last observation date. To estimate stage-specific survival rates, we exponentiated the incubation daily survival rate across 12 days for Thick-billed Longspur nests and 11 days for Chestnut-collared Longspur nests. For nestling stage survival, we exponentiated the daily survival rate across 10 days for Thick-billed Longspurs and 11 days for Chestnut-collared Longspurs. The product of stage-specific survival rates yielded an overall survival rate for the start of incubation to fledging.

To determine proximity of nesting locations, we used nest GPS coordinates to calculate the distances between each Chestnut-collared Longspur nest and the nearest Thick-billed Longspur nest that occurred within the same year. We compared nest locations to pasture spatial data to determine whether or not nests

occurred within the same pasture in a given year.

A total of 859 nest searches were conducted from 2013 to 2019, including 106 in 2013, 80 in 2014, 66 in 2015, 188 in 2016, 66 in 2017, 120 in 2018, and 169 in 2019. Across all years, we detected 293 nests, with 138 of these nests fledging at least 1 young (Table 1). A total of 140 nests failed due to predation ($n = 36$), weather ($n = 2$), and unknown causes ($n = 102$). Fates for 15 nests were undetermined. We observed nests from Thick-billed Longspurs in all years and Chestnut-collared Longspurs in 2013, 2017, and 2018 (Table 1). For the 3 years when Thick-billed Longspurs and Chestnut-collared Longspurs co-occurred, we found a total of 125 Thick-billed Longspur nests (36 in 2013, 54 in 2017, and 35 in 2018) and 34 Chestnut-collared Longspur nests (17 in 2013, 15 in 2017, and 2 in 2018).

Survival rates varied by nest stage and year for both species. Incubation survival rates ranged from 0.45 (95% CI: 0.29–0.68) to 0.61 (95% CI: 0.39–0.93) for Thick-billed Longspurs and 0.50 (95% CI: 0.26–0.90) to 0.81 (95% CI: 0.61–1.08) for Chestnut-collared Longspurs (Table 2). Thick-billed Longspur nestling survival rates ranged from 0.39 (95% CI: 0.20–0.73) to 0.88 (95% CI: 0.75–1.02). Chestnut-collared Longspur nestling survival rates ranged from 0.72 (95% CI: 0.45–1.13) to 0.90 (95% CI: 0.74–1.10). The estimated nest success for incubation and nestling stages combined was 0.19–0.43 for Thick-billed Longspurs and 0.36–0.73 for Chestnut-collared Longspurs (Table 2). We excluded 7 Thick-billed Longspur nests and 2 Chestnut-collared Longspur nests from analysis because they were observed only during the nest-building or egg-laying stages. We were unable to estimate nest success

TABLE 2. Mayfield daily survival rates (DSR) with standard errors (SE) and 95% confidence intervals (95% CI) for incubation and nest stages of Chestnut-collared Longspur (CCLO) and Thick-billed Longspur (TBLO) nests near Roundup, Montana, USA. Only 2 CCLO nests were located in 2018; thus, we did not estimate nest survival rates for 2018 CCLO nests. Incubation stage survival rates were based on an 11-day incubation period for CCLO and a 12-day incubation period for TBLO. Nestling stage survival rates were based on an 11-day nestling period for CCLO and a 10-day nestling period for TBLO. Overall nest success was calculated as the product of the incubation and nestling stage success rates.

Species	Year	Incubation stage			Nestling stage			Overall nest success (95% CI)	
		n	DSR	SE	Overall (95% CI)	n	DSR		SE
CCLO	2013	11	0.938	0.03	0.50 (0.26–0.90)	10	0.970	0.02	0.72 (0.45–1.13)
	2017	12	0.981	0.01	0.81 (0.61–1.08)	12	0.991	0.01	0.90 (0.74–1.10)
TBLO	2013	26	0.947	0.01	0.52 (0.36–0.75)	18	0.956	0.02	0.64 (0.43–0.94)
	2014	35	0.937	0.02	0.46 (0.29–0.70)	33	0.987	0.01	0.88 (0.75–1.02)
	2015	20	0.944	0.02	0.50 (0.30–0.83)	16	0.910	0.03	0.39 (0.20–0.73)
	2016	36	0.935	0.02	0.45 (0.29–0.68)	27	0.954	0.03	0.62 (0.46–0.85)
	2017	39	0.951	0.01	0.55 (0.39–0.76)	41	0.975	0.01	0.78 (0.64–0.94)
	2018	31	0.942	0.02	0.49 (0.33–0.72)	21	0.947	0.02	0.58 (0.39–0.84)
	2019	17	0.959	0.02	0.61 (0.39–0.93)	16	0.928	0.03	0.47 (0.27–0.81)

for Chestnut-collared Longspurs in 2018 due to low sample size.

Chestnut-collared Longspur nests were frequently found in the same pasture as Thick-billed Longspur nests; a total of 28 Chestnut-collared Longspur nests shared pastures with 62 Thick-billed Longspur nests. The mean distance between Chestnut-collared Longspur nests and the nearest Thick-billed Longspur nest was 370 m (SE = 95 m, $n = 33$), and the distances ranged from 32 to 2230 m. Of the nests found, there were 12 individual Chestnut-collared Longspur nests located <100 m from Thick-billed Longspur nests. One Thick-billed Longspur nest and one Chestnut-collared Longspur nest did not have locations recorded and were not included in distance measurements.

The nest success estimates in our study suggest that central Montana rangelands can provide breeding habitat that may be suitable for both Thick-billed and Chestnut-collared Longspurs. Our overall nest success estimates for both species were slightly higher than or similar to those reported in other regions, including 0.22 in Saskatchewan and 0.11–0.26 in Colorado for Chestnut-collared Longspurs (Davis 2003, Sedgwick 2004a), and 0.27–0.75 in Colorado for Thick-billed Longspurs (Sedgwick 2004b). Generalized linear approaches also yielded nest success rates similar to our estimates: 0.31 for Chestnut-collared Longspurs in Montana (Jones et al. 2010) and 0.20–0.24 for Thick-billed Longspurs in Colorado and Montana (Conrey et al. 2016, Swicegood et al. 2022). Our estimates for Chestnut-collared Longspur nest success are notably higher than in previous studies, but small sample sizes ($n = 15–17$ nests) limit strong inference. Incubation survival rates were generally lower than nestling survival rates for both species. The interannual variability observed in our nest success estimates may reflect variable or interactive effects of annual weather, population density, or predator patterns (Fogarty et al. 2017, Crombie and Arcese 2018, Schroeder et al. 2022).

While previous studies have examined habitat associations, abundance, and distribution of Thick-billed and Chestnut-collared Longspurs (Augustine and Baker 2013, Lipsey and Naugle 2017, Pulliam et al. 2020, Muller and Ross 2022), knowledge regarding the nesting ecology of these species remains limited (Somershoe 2018). Our observations of these species nesting within 100 m of each other suggest that our study area may provide sufficient variability in vegetation to

satisfy the differing microhabitat preferences of Thick-billed and Chestnut-collared Longspurs. Our study area occurs where the Northern Great Plains intersects the sagebrush steppe, resulting in an amalgamation of shrublands and mixed-grass prairie (Montana Natural Heritage Program 2017). It is possible that the intermixing of these ecosystems creates structural diversity within the vegetative community that can meet the microhabitat nesting needs of both Thick-billed and Chestnut-collared Longspurs, thereby facilitating nesting co-occurrence at finer scales (Davis 2005, Snyder and Bly 2009).

Identifying regions that support viable breeding songbird populations is a key step toward reversing current songbird declines. Conducting long-term studies may be particularly important for linking habitat quality to nest success or other vital rates, as many studies are limited to 2–3 years and may not capture the full variability of a given vital rate. For instance, Thick-billed Longspur nest success rates in our study were notably higher for 2013–2014 compared to 2015–2016, which, if observed independently, may have resulted in different conclusions about nest success and habitat suitability. Our 7-year data set provides a more robust characterization of nest success, yielding more compelling evidence for the capacity of this region to support viable populations of Thick-billed and Chestnut-collared Longspurs. Moreover, Montana is predicted to be a stronghold for grassland birds under future climate change scenarios (Grand et al. 2019). Additional research that pairs nest outcomes with multiscale habitat data (e.g., vegetation, weather, patch fragmentation, landscape composition, etc.) is an important next step to better elucidate factors that promote successful reproduction in our study area. More importantly, preventing further habitat loss will be essential to preserving the conservation value of this landscape for both Chestnut-collared and Thick-billed Longspurs, as well as other grassland songbirds.

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