The Wilson Journal of Ornithology 122(3):455–464, 2010

REPRODUCTIVE BIOLOGY OF A GRASSLAND SONGBIRD COMMUNITY IN NORTHCENTRAL MONTANA

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ABSTRACT.—Successful conservation of grassland bird populations requires basic information on their breeding biology; in particular, information from undisturbed native prairie over an extended period of time. We present data collected at Bowdoin National Wildlife Refuge in northcentral Montana on the reproductive biology of six grassland bird species that breed in mixed-grass prairie: Sprague's Pipit (*Anthus spragueii*), Savannah (*Passerculus sandwichensis*), Grasshopper (*Ammodramus savannarum*), and Baird's (*A. bairdii*) sparrows, Chestnut-collared Longspur (*Calcarius ornatus*), and Western Meadowlark (*Sturnella neglecta*). Basic measures of reproductive biology are presented, including estimates of nest density, phenology, fecundity, parasitism rates, and nest success, and how these and other characteristics varied across years. Nests (n = 1,494) of the six focal species accounted for 98% of all passerine nests found during 1997–2007; Chestnut-collared Longspurs (51%) were the dominant breeding species. Total nest density across years ranged from 20 to 41 nests per 40 ha (CV = 26%) on unburned sites. Mean clutch initiation date and clutch size varied little across years; however, clutch size tended to decrease over the course of a season, regardless of bird species. Daily nest survival rates did not differ markedly among bird species, but did vary substantially among years, suggesting that year-dependent factors were affecting nest success among all species similarly. *Received 20 December 2008. Accepted 28 February 2010.*

Declines in grassland bird populations have been consistently greater and geographically more widespread than in any other avifaunal group in North America (Knopf 1996, Askins et al. 2007, Sauer et al. 2008), which has been particularly evident for breeding endemics of the northern mixed-grass prairie (Knopf 1996). This has been attributed to many factors, including habitat conversion and fragmentation (Askins et al. 2007), woody vegetation encroachment (Houston and Schmutz 1999), removal of native grazers (Knopf 1994, 1996) and fire (Higgins 1984), and increased predation and parasitism (Basore et al. 1986, Davis and Sealy 2000).

Conservation of grassland bird populations requires basic information on their breeding biology, especially data from undisturbed native prairie over an extended period of time. Large expansive areas of shortgrass and mixed-grass prairies still exist in the western portion of the Great Plains, including northcentral Montana, where these grasslands are relatively intact. In addition, northern prairie grasslands are fundamentally dynamic. Local temporal variability in grassland conditions are largely a function of weather, which can influence plant community structure and composition, both within- and between seasons (Igl and Johnson 1999, Winter et al. 2005, Askins et al. 2007). Fluctuations in habitat conditions result in notable shifts in local bird population densities (Igl and Johnson 1999, Winter et al. 2005) as many native grassland bird species adapt to shifting habitat conditions with nomadic behavior (Clark and Shutler 1999, Ahlering and Johnson 2006, Jones et al. 2007). Consequently, long-term studies focusing on the same population can be instrumental to understanding how reproductive characteristics vary over time.

We studied six species, two of which, Sprague's Pipit (*Anthus spragueii*) and Baird's Sparrow (*Ammodramus bairdii*) are breeding endemics to the northern mixed-grass prairie, and a third, Chestnut-collared Longspur (*Calcarius ornatus*), breeds only in the short to mixed-grass prairie of the western and northern Great Plains. These species have been the subject of recent studies on their reproductive biology (Davis and Sealy 1998, Winter 1999, Davis 2003), and on habitat and management effects (Madden et al. 1999, Davis 2005). However, few studies have occurred in Montana (Hill and Gould 1997, Robbins and Dale 1999, Green et al. 2002), or over an extended period of years. Savannah (*Passerculus sandwichensis*), and Grasshopper (*Ammodramus savannarum*) sparrows, and Western Meadowlarks (*Sturnella neglecta*) have been well-studied

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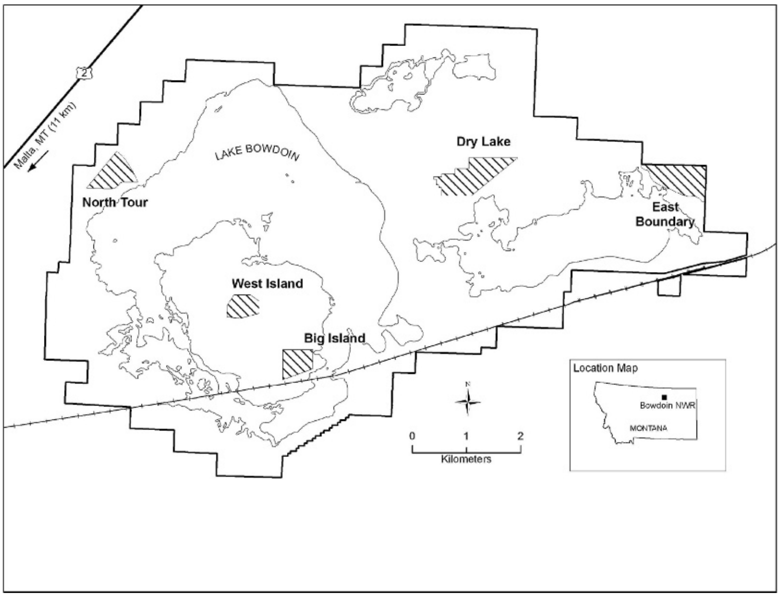

FIG. 1. Study sites at Bowdoin National Wildlife Refuge, northcentral Montana.

throughout much of their range, but relatively few data for these species are available from the northern mixed-grass prairie (Wheelwright and Rising 1993, Lanyon 1994, Vickery 1996).

We present 11 years of data on the reproductive biology of six grassland bird species that breed in mixed-grass prairie of northcentral Montana: Sprague's Pipit; Savannah, Grasshopper, and Baird's sparrows; Chestnut-collared Longspur; and Western Meadowlark. Our objectives were to characterize: (1) songbird community structure, (2) nesting phenology, (3) fecundity, (4) brood parasitism rates and nest success, and (5) to describe how these characteristics varied across years.

METHODS

Study Area.—Our study was conducted during 1997–2007 at Bowdoin National Wildlife Refuge (NWR) in Phillips County, near the town of Malta in northcentral Montana (48° 24′ N, 107° 39′ W; ~750 m asl). The study area consisted of five permanent sites (26–59 ha) totaling 218 ha of flat to gently rolling native mixed-grass prairie (Fig. 1). Data for this analysis were collected at four sites beginning in 1997. One of these sites partially (3 ha) burned in a wildfire in 1994, and was then prescribed burned during spring 2004; a second site was prescribed burned in spring 2007 and was not monitored during 2004. A fifth site, which had been prescribed burned during spring 2000, was added in 2001. No other burning events have occurred on the study sites since refuge documentation began in 1936. Grazing by cattle was gradually phased out during 1973–1977.

The climate is continental and semiarid, characterized by strong winds and high evaporation rates. Mean long-term annual and seasonal (May–Jul) precipitation totals are 34 and 18 cm, respectively (National Climatic Data Center 2007). Mild drought conditions prevailed during the study period; mean annual and seasonal precipitation totals were 32 and 14 cm, respectively (National Climatic Data Center 2007). The plant community was dominated by western wheatgrass (*Pascopyrum smithii*), needle-and-thread (*Stipa comata*), blue grama (*Bouteloua gracilis*), and clubmoss (*Selaginella densa*). Invasive plant species were isolated and sparse. Shrubs (*Sarcobatus vermiculatus*, *Artemisia cana*, *Ceratoides lanata*) were sparse, and trees absent, except sporadically outside the periphery of two study sites.

Photographic records at Sprague's Pipit nests ($n = 5$) documented Northern Harrier (*Circus cyaneus*), garter snake (*Thamnophis* spp.), Western Meadowlark, and deer mice (*Peromyscus* spp.) preying upon nestlings during this study (S. L. Jones, unpubl. data). Other potential nest predators have been observed on, or within, the immediate vicinity of our study sites, including:

American badger (*Taxidea taxus*), long-tailed weasel (*Mustela frenata*), red fox (*Vulpes vulpes*), coyote (*Canis latrans*), mice and voles (*Zapus*, *Reithrodontomys*, and *Microtus*), Richardson's ground squirrel (*Spermophilus richardsonii*), bullsnake (*Pituophis melanoleucus*), prairie rattlesnake (*Crotalus viridis*), gulls (*Larus* spp.), Short-eared Owl (*Asio flammeus*), Loggerhead Shrike (*Lanius ludovicianus*), and Black-billed Magpie (*Pica hudsonia*).

Nest Searching.—Sites were searched for nests 3–5 times per week from early May through late July in an attempt to locate all active nests each year. Search techniques (% successful) included behavioral observations (3%) (Martin and Geupel 1993), opportunistic foot flushes (36%), and rope dragging (61%) (Davis 2003, Dieni and Jones 2003). Nests were marked for relocation by placing a discrete strip of plastic flagging on the ground ~2.5 m on either side of the nest. Nests were monitored every 2–4 days until the nesting outcome was ascertained. Nesting stage at initial discovery was assigned by candling eggs (Lokemoen and Koford 1996) or estimating age of nestlings (Jongsomjit et al. 2007). Nesting outcomes were: (1) successfully fledged at least one young of the parental species, (2) depredated, (3) abandoned (eggs or nestlings left permanently unattended), or (4) unknown. Observations of fledglings within 3 days of expected fledging, the presence of feces and feather scales in the nest, fledglings near the nest, and adults uttering alarm calls nearby or feeding new fledglings within 50 m of the nest were treated as evidence of reproductive success. Predation was assumed when the nest, eggs or nestlings too young to fledge disappeared or were destroyed.

Statistical Analysis.—Number of nests located for each focal bird species was summarized only for the three sites which had not been disturbed by prescribed fire to quantify annual variation of nesting density. Site effects were ignored given the relatively close spatial proximity of the study sites.

The nest was the primary sample unit for the analysis of reproductive parameters and nest success. Clutch initiation dates (CID) were estimated by calculating the date of clutch initiation from egg or nestling age or from known dates of major events (e.g., hatching). Reproductive parameters are reported using standard measures of central tendency. Data variation was summarized using the coefficient of variation (CV = SD/mean; Zar 1999); annual variation for many parameters was summarized only for the dominant species with adequate sample sizes. Trend lines (across years) were fit using the method of least squares; strength of trends was characterized using simple beta (*b*) and correlation (Pearson *r*) coefficients.

We estimated nest daily survival rates (DSR) using the survival model in program MARK (White 2008) for the six focal bird species, and to examine how DSR varied temporally across years (1997–2007). Program MARK uses a generalized linear approach to modeling DSR and maximum likelihood estimation to derive model coefficients and sampling variances (Dinsmore et al. 2002, Rotella et al. 2004). Regression models were constructed using the logistic transformation (logit) as the link function and natural logs [ln(DSR/1-DSR)]. Bird species and year were treated as nominal-scale variables (6 and 11 levels, respectively) with each level introduced into the regression model as an artificial explanatory variable and 0 or 1 coding; second-order interactions between species and year were added with the appropriate cross-product terms. One candidate model set was evaluated within an information-theoretic framework (Burnham and Anderson 2002). Program MARK was used to calculate Akaike's Information Criterion corrected for small sample sizes (AIC_c), ranking the fit of each model in ascending order of AIC_c values. Estimates for each species and year were calculated using the model-averaging approach (Burnham and Anderson 2002) weighted according to that model's likelihood in the set (normalized Akaike weight). The intercept-only model (where the regression coefficient was set to zero) was included in a set with the covariate of interest (species or year), which served to reduce model-selection bias of the estimate (Burnham and Anderson 2002). A point estimate of nest success was calculated as DSR raised to the mean number of days of the nesting period (incubation and nestling stages combined) for each species (Rotella 2007).

RESULTS

Nine species of passerines were actively breeding on our study area. Nests (n = 1,494) of the six focal species accounted for 98% of all passerine nests found during 1997–2007. Only a small number of nests of Horned Lark (*Eremophila alpestris*; n = 5), Lark Bunting (*Calamos-*

TABLE 1. Annual variation in nesting totals for six songbird species, Bowdoin National Wildlife Refuge, Montana. Numbers of nests discovered in the three undisturbed sites were summarized across years (1997–2006). Total nests were summarized across all songbird species encountered. Values are adjusted per 40 ha. Linear trends in nest totals across years are summarized using Pearson (*r*) and beta (*b*) coefficients.

Statistic	Sprague's Pipit	Savannah Sparrow	Grasshopper Sparrow	Baird's Sparrow	Chestnut-collared Longspur	Western Meadowlark	Total nests
Mean	2.7	4.6	2.7	1.5	15.4	2.6	30.4
CV	0.49	0.30	0.33	1.05	0.31	0.46	0.25
Min	1.3	2.8	1.5	0	10.7	0.8	20.6
Max	5.3	7.4	4.1	4.8	22.4	4.1	41.2
n	94	164	97	52	547	92	1,075
r	0.16	−0.64	0.14	−0.76	−0.53	−0.61	−0.56
b	0.1	−0.3	0.0	−0.4	−0.8	−0.2	−1.3

piza melanocorys; *n* = 7), and Vesper Sparrow (*Pooecetes gramineus*; *n* = 18) were found. Chestnut-collared Longspurs were the dominant breeding species accounting for over 51% of all passerine nests discovered over all years, followed by Savannah Sparrow (17%), Sprague's Pipit (8.4%), Grasshopper Sparrow (8.1%), Western Meadowlark (7.8%), and Baird's Sparrow (6%). Mean rank in nest abundance across all years followed a similar order: Chestnut-collared Longspur (1.0, CV = 0.0), Savannah Sparrow (2.2, CV = 0.20), Western Meadowlark (3.9, CV = 0.27), Grasshopper Sparrow (4.1, CV = 0.19), Sprague's Pipit (4.2, CV = 0.33), and Baird's Sparrow (5.6, CV = 0.18).

Annual variation in total nests was summarized collectively for three unburned study sites (Table 1). Annual variation (CV) in nest density ranged from 1.05 for Baird's Sparrow to 0.30 for Savannah Sparrow among focal species. Variability in total songbird nest density was moderate (CV = 0.25) ranging from 41 nests/40 ha in 1997 to 21 nests/40 ha in 2001. A modest declining trend for total songbird nests/40 ha was evident (*b* = −1.3, *r* = −0.56) across all years. This trend was pronounced for Baird's Sparrow (*r* = −0.76), but also evident for Savannah Sparrow (*r* = −0.64), Western Meadowlarks (*r* = −0.61), and Chestnut-collared Longspurs (*r* = −0.53). Nests were primarily discovered during incubation (67%) with frequency of nests discovered generally decreasing thereafter. Relatively few nests were discovered during the nest-building phase (Fig. 2).

Reproductive Parameters.—The CID frequency distribution for Chestnut-collared Longspurs was multimodal across all years, exhibiting three peaks. Bimodal distributions were evident for

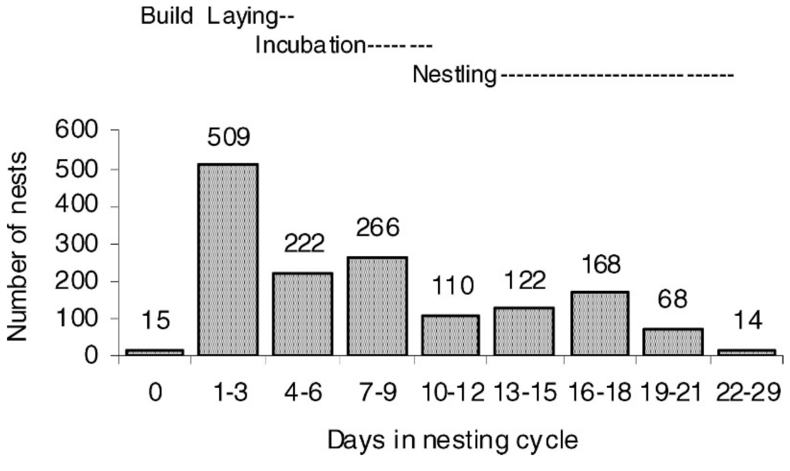

FIG. 2. Frequency distribution of nest age-intervals at time of discovery, Bowdoin National Wildlife Refuge, Montana, 1997–2007 (*n* = 1,494). Nests were primarily located during incubation with frequency of nests generally decreasing thereafter. Relatively few nests were located during the nest-building phase.

TABLE 2. Frequency distributions for clutch initiation dates (CID) for six songbird species at Bowdoin National Wildlife Refuge, Montana, 1997–2007. Values include peaks (modes), mean, and median nesting dates. Nesting period includes the range of activities observed across years for each species from the earliest CID date to last nest fledged. Frequency distributions were multimodal for three species and generally positively skewed towards early season breeding for all species.

Species	Nest peaks	Mean	Median	Earliest	Latest	Potential nesting period
Sprague's Pipit	23 May	5 Jun	25 May	7 May	31 Jul	07 May–25 Aug
Savannah Sparrow	24 May, 27 Jun	6 Jun	2 Jun	11 May	19 Jul	11 May–09 Aug
Grasshopper Sparrow	27 May	13 Jun	16 Jun	18 May	17 Jul	18 May–06 Aug
Baird's Sparrow	30 May	11 Jun	9 Jun	14 May	21 Jul	14 May–10 Aug
Chestnut-collared Longspur	21 May, 6 Jun, 15 Jun	7 Jun	7 Jun	30 Apr	19 Jul	30 Apr–10 Aug
Western Meadowlark	24 May, 2 Jun, 7 Jun	4 Jun	4 Jun	30 Apr	14 Jul	30 Apr–07 Aug

Savannah Sparrows and Western Meadowlarks; the remaining species were unimodal. All CID frequencies were positively skewed towards early-season breeding. On average, Sprague's Pipits were the earliest to nest (median date = 25 May) and Grasshopper Sparrows were the latest (median date = 16 Jun) (Table 2). All species ended clutch initiation by the end of July. The earliest fledging date observed was 26 May (Chestnut-collared Longspur) and the latest was 25 August (Sprague's Pipit). Variation in mean CID across years was low for Chestnut-collared Longspurs (SD = 2.9 days) and higher for Savannah Sparrows (SD = 5.6 days). The trend in CID across years was extremely weak for either species ($|b| \leq 0.20$ d, $|r| < 0.12$).

Variability (CV ≤ 0.18) in incubation and nestling phase duration was low, regardless of species (Table 3). Mean clutch size across all years ranged from 4.1 eggs (Chestnut-collared Longspurs) to 4.6 eggs (Sprague's Pipits). Mean clutch size did not vary considerably across years for either Chestnut-collared Longspurs (CV = 0.04) or Savannah Sparrows (CV = 0.06). Clutch size tended to decrease over the course of a season, regardless of bird species, although Sprague's Pipits and, to a lesser extent, Chestnut-collared Longspurs had increased clutch sizes during the first month of the breeding season (Fig. 3). Hatching rate (% of total eggs laid that hatched) across all years ranged from 88% for Chestnut-collared Longspurs and Grasshopper Sparrows to 78% for Savannah Sparrows. Hatching rates were similar for Sprague's Pipits (85%), Baird's Sparrows (84%), and Western Meadowlarks (82%).

Mean number of nestlings across all years ranged between 3.5 for Savannah Sparrows to 4.0

TABLE 3. Nest stage duration and reproductive parameters, by songbird species at Bowdoin National Wildlife Refuge, Montana, 1997–2007. Values represent mean ± CV (*n*; range). Fledged/nest represents the number of young fledged across all nests, regardless of nesting outcome.

	Nest stage (days)		Reproductive parameters			
Species	Incubation	Nestling	Clutch size	No. of nestlings	No. fledged/ successful nest	Fledged/nest
Sprague's Pipit	12.2 ± 0.12 (85; 7–15)	12.9 ± 0.18 (19; 9–17)	4.6 ± 0.17 (129; 1–6)	4.0 ± 0.26 (97; 1–6)	3.4 ± 0.35 (49; 1–6)	1.30 ± 1.07
Savannah Sparrow	11.6 ± 0.11 (184; 8–15)	10.1 ± 0.16 (73; 7–14)	4.3 ± 0.23 (260; 1–6)	3.5 ± 0.37 (191; 1–6)	3.2 ± 0.41 (101; 1–6)	1.23 ± 0.94
Grasshopper Sparrow	10.9 ± 0.14 (86; 7–13)	9.7 ± 0.17 (26; 7–12)	4.3 ± 0.24 (123; 0[a]–6)	3.9 ± 0.28 (95; 1–6)	3.6 ± 0.33 (64; 1–5)	1.89 ± 1.56
Baird's Sparrow	11.0 ± 0.10 (62; 7–14)	9.6 ± 0.11 (27; 8–11)	4.3 ± 0.19 (90; 2–6)	3.7 ± 0.31 (70; 1–5)	3.4 ± 0.36 (40; 1–5)	1.52 ± 1.31
Chestnut-collared Longspur	10.9 ± 0.12 (567; 7–15)	11.1 ± 0.16 (185; 7–15)	4.1 ± 0.20 (770; 1–7)	3.6 ± 0.27 (627; 0[a]–6)	3.4 ± 0.32 (342; 0[a]–5)	1.50 ± 1.37
Western Meadowlark	12.9 ± 0.12 (78; 8–15)	12.7 ± 0.10 (31; 9–16)	4.4 ± 0.30 (119; 0[a]–7)	3.8 ± 0.40 (89; 1–6)	3.2 ± 0.47 (46; 1–5)	1.24 ± 0.82

[a] Brown-headed Cowbird (*Molothrus ater*) only.

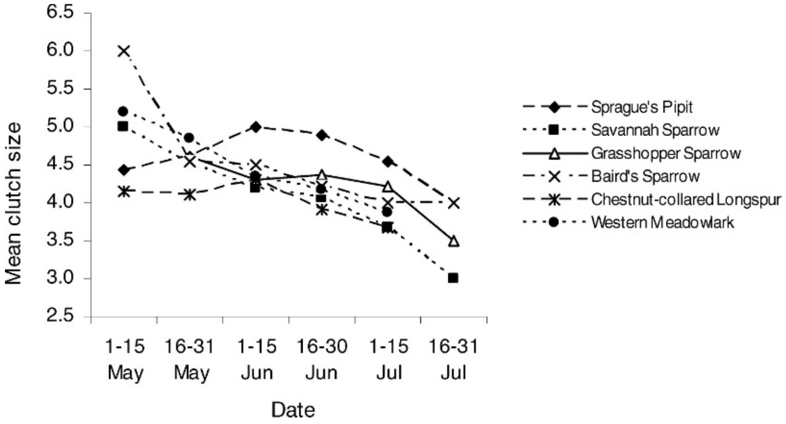

FIG. 3. Mean clutch size plotted against date by species across all years (1997–2007), Bowdoin National Wildlife Refuge, Montana. Mean clutch size generally decreased for each species as the nesting season progressed.

for Sprague's Pipits (Table 3). Grasshopper Sparrows had the highest fledging rate (1.9) across all nests in all years while Savannah Sparrows and Western Meadowlarks had the lowest (1.2) (Table 3). Variation in mean fledglings/nest across years was low for Chestnut-collared Longspurs (CV = 0.20) with a modest decreasing trend across years ($b = -0.05$, $r = -0.59$). This statistic was more variable for Savannah Sparrows (CV = 0.45), but with no discernable trend ($r = -0.09$).

Nest Success.—DSR across all species and years was estimated at 0.947 (SE = 0.002). There was little statistical support for species-specific variation in DSR (Table 4). Model-averaged estimates for each species (Table 5) indicated little variation in DSR among species. However, variation in DSR across years was evident, suggesting a decline during the study period ($b = -0.002$, $r = -0.54$) (Fig. 4). There was little statistical support for an interaction between species and year (Table 4).

Nest depredation accounted for 82% of all known nest failures with most (71%) during the nestling stage. Desertion (abandonment) was judged to be the cause for 18% of all known nest failures. Cause of abandonment was discernable in only 27% of these cases; 25% ($n = 38$) were attributed to severe weather (e.g., heavy rain, hailstorms), 1% ($n = 2$) to observer activities, and 1% ($n = 2$) to Brown-headed Cowbird brood parasitism. Brown-headed Cowbird parasitism rates ranged from 2% for Chestnut-collared Longspurs to 26% for Western Meadowlarks (Table 6).

TABLE 4. Model set exploring the relationship between bird species (6 levels) and year (1997–2007) at Bowdoin National Wildlife Refuge, Montana on nest daily survival rate (DSR) using Akaike's Information Criterion, corrected for small sample sizes (AIC_c). Delta AIC_c (AIC_c model i – AIC_c minimum), Akaike weight (w_i), and number of parameters (K) are included for each model.

Model	Δ AIC_c	w_i	K
Year	0.0	0.66	11
Species + year	1.5	0.31	16
Intercept	6.8	0.02	1
Species	10.7	0.00	6
Species*year	10.7	0.00	63

DISCUSSION

Songbird community structure based on nesting density was relatively stable across the 11-year period of this study. Chestnut-collared Longspurs were clearly the dominant nesting species every year. Savannah Sparrows were the second most abundant bird species during all but 2 years, while Baird's Sparrows were least abundant among focal species during all but 2 years. Few to no nests of shortgrass prairie obligates, such as Horned Lark or McCown's Longspur (*Calcarius mccownii*) were located. Chestnut-collared Longspurs generally breed in drier, shortgrass to short–mixed-grass prairie, while Sprague's Pipits and Baird's Sparrows range across the breadth of mixed-grass prairie grassland types (Knopf 1996). Our assemblage of breeding songbirds, in addition to plant community composition and structure (Dieni and Jones 2003), classify our study area as

TABLE 5. Estimated nest DSR for six bird species across all years at Bowdoin National Wildlife Refuge, Montana, 1997–2007. Standard errors (SE), lower (LCI) and upper (UCI) 95% confidence limits, and number of nests (*n*) are included. Nest success equals DSR raised to the mean number of days of the nesting period (incubation and nestling stages combined) for each species.

Species	DSR	SE	LCI	UCI	*n*	Nesting period	Nest success
Sprague's Pipit	0.947	0.003	0.942	0.952	128	25.1	0.27
Savannah Sparrow	0.946	0.004	0.938	0.953	255	21.7	0.25
Grasshopper Sparrow	0.948	0.004	0.940	0.955	121	20.6	0.39
Baird's Sparrow	0.947	0.003	0.940	0.953	90	20.6	0.32
Chestnut-collared Longspur	0.947	0.002	0.943	0.951	759	22.0	0.31
Western Meadowlark	0.947	0.003	0.941	0.952	118	25.6	0.25
Totals	0.947	0.002	0.943	0.950	1,471	22.3	0.30

xeric short–mixed-grass prairie (Knopf 1996, Askins et al. 2007).

Breeding Bird Survey data indicate long-term (1966–2007) declines in rangewide populations for all our focal bird species (Sauer et al. 2008). In particular, rangewide populations of two mixed-grass endemics, Sprague's Pipit (-3.9, $P = 0.00$, $n = 169$) and Baird's Sparrow (-3.4, $P = 0.01$, $n = 141$), as well as Chestnut-collared Longspur (-2.8, $P = 0.00$, $n = 160$) have exhibited steep declines (Sauer et al. 2008). We recorded general declines in nest density for most of our study species on undisturbed study sites, although no discernable trend was observed for Sprague's Pipit or Grasshopper Sparrow. The decline in nesting density of Baird's Sparrow may be a function of drier than normal climatic conditions that prevailed over most of the study period (National Climatic Data Center 2007). Our study area possessed none of the habitat conditions that are commonly the result when the northern mixed-grass prairie is left idle (Madden et al. 1999). The prevalence of invasive plant species and woody-vegetation encroachment remained low, while forbs were abundant during the course of the study (S. L. Jones, unpubl. data). Moreover, xeric mixed-grass prairie historically had lengthy periods without grazing, and natural burn frequencies that often ranged between 8 and 26 years (Askins et al. 2007).

We used nest density as an index to bird abundance to gauge community structure and trend, but nest density clearly does not equate directly to bird or even territorial density. Some species we studied have been documented to have multiple broods in a season. Our population was marked for only a few species and years (Jones et al. 2007); it was not possible in most cases to distinguish single broods by different individuals from multiple broods after a successful nest or re-

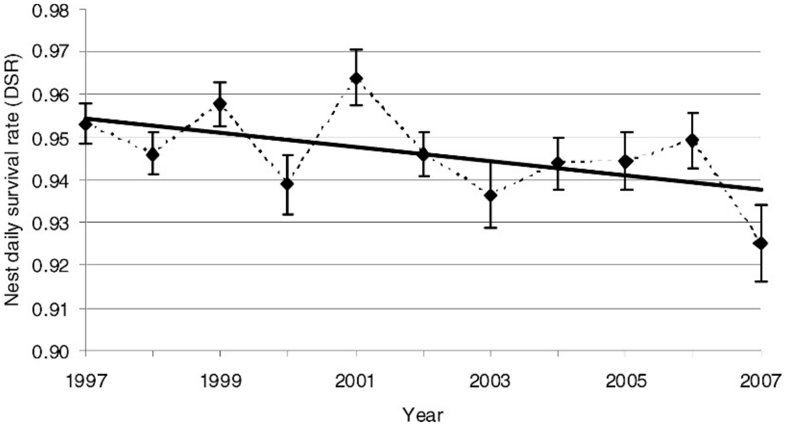

FIG. 4. Annual variation in daily survival rates of songbird nests (DSR ± SE) at Bowdoin National Wildlife Refuge, Montana. There was considerable annual variation in DSR (annual mean = 0.946 ± 0.011 CV). A declining trend in DSR was evident ($b = -0.002$, $r = -0.54$).

TABLE 6. Nesting outcome and parasitism rates for each bird species across all years, 1997–2007 at Bowdoin National Wildlife Refuge, Montana. Most monitored nesting attempts were unsuccessful with the majority of failures attributed to nest predation. Weather events (e.g., hail) were collectively the leading known cause of nest desertion. Parasitism by Brown-headed Cowbirds resulted in only a few nest failures.

						Brown-headed Cowbird parasitism		Known causes of abandonment (*n*)		
Species	Successful	Depredated	Abandoned	Unknown	*n*	Relative frequency	Total cowbirds fledged	Weather	Observer disturbance	Parasitism
Sprague's Pipit	0.37	0.57	0.06	0.00	128	0.02	2	1	0	0
Savannah Sparrow	0.40	0.43	0.17	0.01	260	0.13	17	15	1	1
Grasshopper Sparrow	0.52	0.35	0.12	0.01	123	0.04	2	3	0	0
Baird's Sparrow	0.43	0.42	0.16	0.00	89	0.04	0	4	0	0
Chestnut-collared Longspur	0.44	0.48	0.07	0.01	770	0.02	3	11	0	1
Western Meadowlark	0.40	0.45	0.14	0.00	119	0.26	18	4	1	0
n	637	688	151	13	1,489	91	42	38	2	2

nesting after nest failure. However, Savannah Sparrows, Chestnut-collared Longspurs, and Western Meadowlarks all had multimodal CID distributions suggesting at least some community members may have had several clutches per year. None of the species we studied has been documented with more than two successful broods per year (Wheelwright and Rising 1993, Lanyon 1994, Vickery 1996, Hill and Gould 1997). Sprague's Pipit, and Baird's and Grasshopper sparrows had only single frequency peaks in our CID data, which suggests a tendency towards a single brood per season. This contrasted with Vickery (1996), who reported Grasshopper Sparrows in general have a protracted breeding season, often producing ≥2 broods annually, even in the northern portion of their range. Sprague's Pipit and Baird's Sparrow have only rarely been documented to have multiple broods in a season (Robbins and Dale 1999, Green et al. 2002). Second broods after successfully fledging young have been documented twice for Sprague's Pipit (Sutter 1996, Davis 2009). Re-nesting after nest failure has been rarely documented for this species (Sutter 1996, Davis 2009), as has polygyny ($n = 1$) (Dohms and Davis 2009). Baird's Sparrow in southwest Manitoba (Davis and Sealy 1998) and in our study had a second, smaller nest initiation peak in mid to late June, suggesting second broods or re-nesting attempts; second broods have only been documented twice (Davis and Sealy 1998; S. L. Jones, unpubl. data).

Mean CID for Savannah Sparrows and Chestnut-collared Longspurs varied little across years. Mean clutch size also had little variation among seasons; however, a within-season declining pattern was evident for this parameter for all species. Similar patterns have been documented elsewhere for these bird species (Vickery 1996, Davis and Sealy 1998, Winter 1999, Davis 2003). Sprague's Pipits were a notable exception in our study, where clutch size generally increased during the first month of the breeding season. A similar pattern was also reported for Sprague's Pipit in Saskatchewan (Davis 2003). Clutch size in our study linearly decreased over the course of the breeding season for Western Meadowlarks, which contrasted with a study in Manitoba, where Western Meadowlarks had peak clutch size during mid-season (Lanyon 1994).

Brown-headed Cowbird parasitism rates, except for Western Meadowlark, were relatively low in our study (2–13%). Much higher rates were reported for our focal species in southwest Manitoba: Sprague's Pipit = 18%, Savannah Sparrow = 32%, Grasshopper Sparrow = 29%, Baird's Sparrow = 37%, and Chestnut-collared Longspur = 14% (Davis and Sealy 2000). Our rate for Western Meadowlark (26%) was low compared to rates reported in Manitoba (43%) (Davis and Sealy 2000), and North Dakota (47%) (Koford et al. 2000), but were consistent with reported rates in Saskatchewan (25%) (Davis 2003). Chestnut-collared Longspurs and Sprague's Pipits had the lowest parasitism rates in our study, which is consistent with findings in other studies (Hill and Gould 1997, Davis and Sealy 2000, Davis 2003). Several factors may be responsible for the relatively low levels of parasitism found in our study area (i.e., large patches of continuous grassland, a landscape with few potential perches, relatively little shrub and tree cover, and no cattle grazing). All of these factors directly enhance Brown-headed Cowbird parasitism rates (Davis and Sealy 2000, Koford et al. 2000).

Nest depredation is commonly the single most important factor affecting nesting success in cup-nesting passerines (Ricklefs 1969); depredation rates have been generally high throughout the mixed-grass prairie (Vickery et al. 1992; Winter 1999; Davis 2003, 2005; Winter et al. 2005). Nest predation accounted for the majority of observed nest failures in our study, mainly during the nestling stage. This is a common pattern among passerines; greater parental activity at the nest, as well as greater olfactory cues, noise, and movements by nestlings are thought to increase the likelihood of nest detection by predators (Halupka 1998).

Overall nest success for Sprague's Pipits was estimated to be much higher in southwest Manitoba (47%, Davis and Sealy 1998) than estimated in our study area (27%). Grasshopper Sparrow and Western Meadowlark nesting success rates were comparable to those reported by Lanyon (1994) and Vickery (1996). Our estimate of nest success (32%) for Baird's Sparrow was higher than reported in Saskatchewan (26%, Davis 2003), but lower than in Manitoba (54%, Davis and Sealy 1998). Nest success for Chestnut-collared Longspurs was higher in Alberta (56%, Hill and Gould 1997) than estimated for our study area (44%; Table 6).

DSR estimates did not differ markedly among bird species, suggesting that factors such as weather and the predator community were affecting all bird species equally. Therefore, those elements affecting nest success that vary with year (i.e., predator community or weather) probably influenced the members of this grassland songbird community in a similar manner in a given year.

ACKNOWLEDGMENTS

This project was funded by the U.S. Fish and Wildlife Service, Nongame Migratory Bird Program, Region 6. Field support and resources were provided by J. E. Cornely, C. R. Luna, D. M. Prellwitz, and the staff at Bowdoin National Wildlife Refuge. We thank the many dedicated field assistants who worked on this project over the years: Brice Adams, A. C. Araya, B. S. Atchley, R. R. Conover, Michael Friedrich, Jeanne Hammond, D. I. Hedegaard, Jessica Hinz, B. G. Larson, Rebecca Lind, L. B. Lingohr, S. N. Luttich, Kevin Payne, Heather Sauls, Caroline Stahala, Vicki Trabold, P. N. Wiederrick, and J. K. Wood. We are also grateful to M. T. Green, G. R. Guepel, and J. R. Ruth for insights that contributed to the design and conduct of this study. D. J. Ingold, D. H. Johnson, and an anonymous reviewer provided edits and comments that substantially improved this paper. We thank Mike Artmann for the map in Fig. 1.

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