NESTING ECOLOGY OF GRASSLAND SONGBIRDS: EFFECTS OF PREDATION, PARASITISM, AND WEATHER

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ABSTRACT.—Understanding the breeding ecology of grassland birds is vital for understanding the mechanisms underlying their widespread population declines. We describe the breeding biology of Sprague's Pipit (*Anthus spragueii),* Vesper Sparrow (*Pooecetes gramineus)*, Savannah Sparrow (*Passerculus sandwichensis*), Baird's Sparrow (*Ammodramus bairdii*), and Western Meadowlark (*Sturnella neglecta*) and quantify the effects of nest predation, brood parasitism, and weather on the nest survival of these species in southeastern Alberta. Nest predation was the primary cause of nest failure, accounting for 75% of all nest losses. Daily survival rates were higher during incubation than the nestling stage for the three sparrow species, and nest survival of Baird's Sparrows was highest at intermediate temperatures. For all five species, clutch size, hatching success, and fledging success were within the range of values previously reported for these species in other parts of their range. Brown-headed Cowbirds parasitized nests of all species except Sprague's Pipit, with 4–11% of nests containing cowbird eggs. Savannah Sparrow experienced the highest frequency of brood parasitism and was the only species to successfully fledge cowbird young. Parasitized nests of Savannah Sparrows had reduced clutch size and hatching success, and fledged fewer young compared to non-parasitized nests. The overall cost of parasitism to Savannah Sparrows was at least 1.7 young per successful nest. *Received 21 October 2013. Accepted 16 June 2014.*

Key words: Alberta, clutch size, cowbird parasitism, logistic exposure, mixed-grass prairie, nest survival, reproductive success.

Native grasslands have been reduced to ~20% of their historic area and represent the most drastically altered biome in North America (Samson and Knopf 1994). Historically, much of the loss occurred because of European settlement and agricultural policies that promoted the conversion of grassland to cropland (Samson et al. 2004). The remaining native tracts continue to be threatened by cultivation, fire suppression, woody vegetation, exotic plant species, urbanization, and industrial development (Askins et al. 2007). The loss and degradation of native prairie has resulted in widespread population declines of many grassland bird species (Askins et al. 2007). For example, of the 37 grassland bird species (12 primary and 25 secondary endemic) listed by Knopf (1994), 15 are federally listed as species at risk or are under consideration for listing in Canada (Commitee on the Status of Endangered Wildlife in Canada 2013), and 6 species are federally listed or under consideration for listing as endangered or threatened in the United States (U.S. Fish and Wildlife Service 2013). Our ability to understand the mechanisms underlying declines in these populations is limited by our lack of

information about their breeding biology and reproductive success. While a number of nesting biology studies have been conducted on grassland songbirds (Davis and Sealy 2000, Davis 2003, Jones et al. 2010, Kerns et al. 2010), more data are required from different regions and years to enable an assessment of the spatial and temporal variation in demographic rates. Descriptive data on basic breeding information is vital to the successful design and implementation of management plans and conservation policies (Lande 1988, Fletcher et al. 2006). In particular, determining which factors most influence nest survival and reproductive success is critical for modeling population dynamics (Morrison 2001). An understanding of resource use and breeding ecology, as well as the influence of predators and weather on individuals and populations is particularly important because little can be done to stabilize or enhance populations without an understanding of the mechanisms driving population declines (Vonesh and De la Cruz 2002, Robinson et al. 2004).

Predation and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) are important factors that negatively affect the reproductive success of grassland songbirds (Davis 2003), but rates vary among species and regions (Woolfenden et al. 2004, Fontaine et al. 2007). Predation is typically the primary factor influencing nest success and survival (Martin 1993), however,

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brood parasitism can reduce hatching success and nestling and fledgling survival (Hoover 2003, Rasmussen and Sealy 2006, Goguen et al. 2009). Extreme variations in temperature and precipitation may also negatively influence grassland songbird reproductive success (George et al. 1992), either indirectly through habitat alterations or directly through heat stress or water limitations. Our objectives were to 1) quantify and compare clutch size and clutch initiation dates, 2) determine the extent to which temperature and precipitation influence nest survival, and 3) quantify the extent to which nest predation and brood parasitism influence nest survival and reproductive success of five species of grassland songbirds in southeastern Alberta, Canada.

METHODS

Study Site.—We conducted our study at the Antelope Creek Habitat Development Area (ACHDA) in southeastern Alberta (50° 33′ N, 111° 53′ W; elevation ~760 m) from May to August in 2010 and 2011. The ACHDA and surrounding area consists largely of native, dry mixed-grass prairie and managed wetlands. Native vegetation consists primarily of needle-and-thread (*Hesperostipa comata*) and blue grama grass (*Bouteloua gracilis*), and also includes prickly-pear cactus (*Opuntia polyacantha*), spinystar (*Escobaria vivipara*), sage (*Artemisia* spp.), lesser spikemoss (*Selaginella densa*), and various forbs. Grazing on the native grassland at the ACHDA begins mid-July. Approximately 200 cow-calf pairs are rotated through four paddocks (430–570 ha) with cattle typically spending 24 days in each paddock.

Data Collection.—In 2010, we established 12 plots distributed across all of the ACHDA. Four plots were added in 2011 to increase the area searched for nests. Plot placement was determined by the extent of native grassland cover, and we avoided placing plots in low-lying, flooded areas. Where the terrain allowed, plots were 600 × 300 m and plot size ranged from 14–21 ha (mean ± SD: 17.7 ± 1.7 ha). We marked each study plot with surveyor flags in a 50-m grid to facilitate nest searching and monitoring.

We conducted nest searches from early May to late July in each year. We located nests mostly between 0600–1400 Mountain Daylight Time by systematically dragging a 25-m nylon rope, weighted with metal cans, through each study plot to flush incubating birds from nests (Davis 2003). We concentrated nest-searching efforts shortly after sunrise to increase the likelihood of flushing incubating females (Davis and Holmes 2012). Nests were also located opportunistically while conducting other activities in the area. We recorded nest locations with a hand-held global positioning system unit and placed colored surveyor's flags 5 m north and south of the nest to facilitate relocation. Nest flags were identical to grid flags to reduce the risk of predators using them as cues and were placed just above the average height of the vegetation. We checked nests every 3–4 days until chicks fledged or the nesting attempt failed. We searched each plot for nests five times over the course of the season in both years. We did not conduct nest searches during cold, wet weather and took care to avoid creating paths which ended at a nest to minimize human-induced nest failure. Similarly, we conducted nest checks as quickly as possible to minimize disruption of parental care. We candled eggs (Lokemoen and Koford 1996) to determine clutch initiation dates and to estimate hatching dates to increase the precision of our calculated survival rates (Shaffer 2004). For this same reason, we aged nestlings based on images of known-age young. We considered nest attempts successful if at least one host nestling fledged. Cues such as nestling age on last visit, adult alarm calls, fledglings observed nearby, and the presence of droppings and feather scales in the nest were used as evidence to identify successful nests. For nests with known fate, the midpoint between the last visit when the nest was observed active and the subsequent visit was used to determine exposure days. Exposure days for nests with unknown fate were included up to the last observed active visit (Manolis et al. 2000).

We measured nest visibility by placing a thin 7.5-cm wooden disk divided into eight equal black-and-white sections into the nest cup and counted the number of visible sections from 1 m away in each of the four cardinal directions as well as from 1 m directly overhead (Davis and Sealy 1998, Davis 2005). We averaged the five measurements to derive a single visibility value for each nest with a value of eight being most visible and 0 being least visible. We scored nest visibility along a gradient, which ranged from completely concealed to completely exposed, rather than categorizing a nest as concealed or not based on whether the disk was observable. We obtained temperature and precipitation data from Environment Canada's

weather station in Brooks, Alberta ($50° 33'$ N, $111° 50'$ W), which is ~20 km east of the ACHDA. For the temperature and precipitation variables, we used the mean of nest visit intervals.

Statistical Analyses.—We performed all analyses in SAS Enterprise Guide 4.3 (SAS Institute, Inc. 2010). We combined data from both years for species with <50 nests. We calculated clutch initiation dates based on the age of eggs and young, as well as known hatching dates. We calculated mean clutch size of all nests initiated within a given week (starting 1 May to 23 Jul) by different females of the same species and then regressed this using a general linear model (PROC GLM) weighted by the square root of the number of nests to determine the extent to which mean weekly clutch size varied over the breeding season. Nests were excluded from clutch size analyses if they 1) contained cowbird eggs or young on the first visit, 2) were deserted during the laying stage, or 3) they had fewer than three eggs and were found during the middle of the breeding season or during the nestling or late incubation stage. These criteria were used to omit nests where it was unclear whether the number of eggs or chicks in the nest represented a complete clutch. Nests with fewer than three eggs that were found early or late in the breeding season were included, since females may produce smaller clutches during these portions of the breeding season (Wray et al. 1982).

We used the logistic exposure method (Shaffer 2004) to determine the extent to which daily survival rate varied as a function of temporal (nest age, date, and year) and environmental factors (temperature and precipitation). We examined models including an interactive effect of year and age for species with ≥50 nests to ensure there were no effects dependent on the year of the study. We combined years if we found no support for an interactive effect of year on daily nest survival rate or if the direction of the response was the same in both years. Otherwise we analyzed years separately. Our temporal models ($n = 12$) included linear effects of age and date, quadratic effect of age, cubic effect of age, a null (constant survival), interactive effects of age and date, and a global model. Environmental models ($n = 6$) included linear effects of precipitation and temperature, as wells as a quadratic effect of temperature, a null, and a global model. We combined the top temporal model with environmental models to determine the relative impor-

tance of environmental factors on nest survival. We used Akaike's Information Criteria adjusted for small sample sizes (AIC_c) to rank models (Burnham and Anderson 2000). We considered the model with the lowest AICc value to be the best fit model of those considered. For model selection purposes, we calculated 85% confidence limits to identify uninformative model parameters (Arnold 2010). Because of model selection uncertainty among temporal models, we performed model averaging on all models that were better than null and had weights greater than zero. We compared hatching success (number of eggs hatched per nest), fledging success (mean number of young fledged per nest and per successful nest), clutch size (number of eggs laid in a nest), and predation rates of parasitized and non-parasitized Savannah Sparrows' nests using the Student's t-test (PROC TTEST). Savannah Sparrow (*Passerculus sandwichensis*) was the only species included in this comparison, because nests of other species parasitized by cowbirds were low in number. Nest visibility values and hatching and fledging rates from non-parasitized, parasitized, and multiply parasitized nests are presented as mean ± standard deviation.

RESULTS

We located 533 nests of 23 species during the 2 years of study. We focus on the five songbird species that comprised ~98% of the total number of songbird nests ($n = 332$) and for which at least 20 nests were found (Hensler and Nichols 1981): Sprague's Pipits (*Anthus spragueii*; $n = 21$), Vesper Sparrows (*Pooecetes gramineus*; $n = 53$), Savannah Sparrows ($n = 190$), Baird's Sparrows (*Ammodramus bairdii*; $n = 35$), and Western Meadowlarks (*Sturnella neglecta*; $n = 26$).

Clutch Initiation and Clutch Size.—Earliest clutch initiation dates ranged from 8–19 May and peaked during 28 May to 7 June for all five species in both years (Fig. 1). Nest initiation continued until the end of July for all five species. On average, Western Meadowlarks initiated nests earliest and Baird's Sparrows initiated nests latest (Fig. 1). Vesper Sparrows tended to lay the smallest clutches, whereas Western Meadowlark laid the largest (Table 1). Vesper and Baird's sparrows experienced a decrease in clutch size over the breeding season; however, these relationships were highly variable ($-0.094 ± 0.05$; $-0.081 ± 0.07$, respectively). Clutch sizes of Savannah Sparrows, Sprague's Pipits, and Western
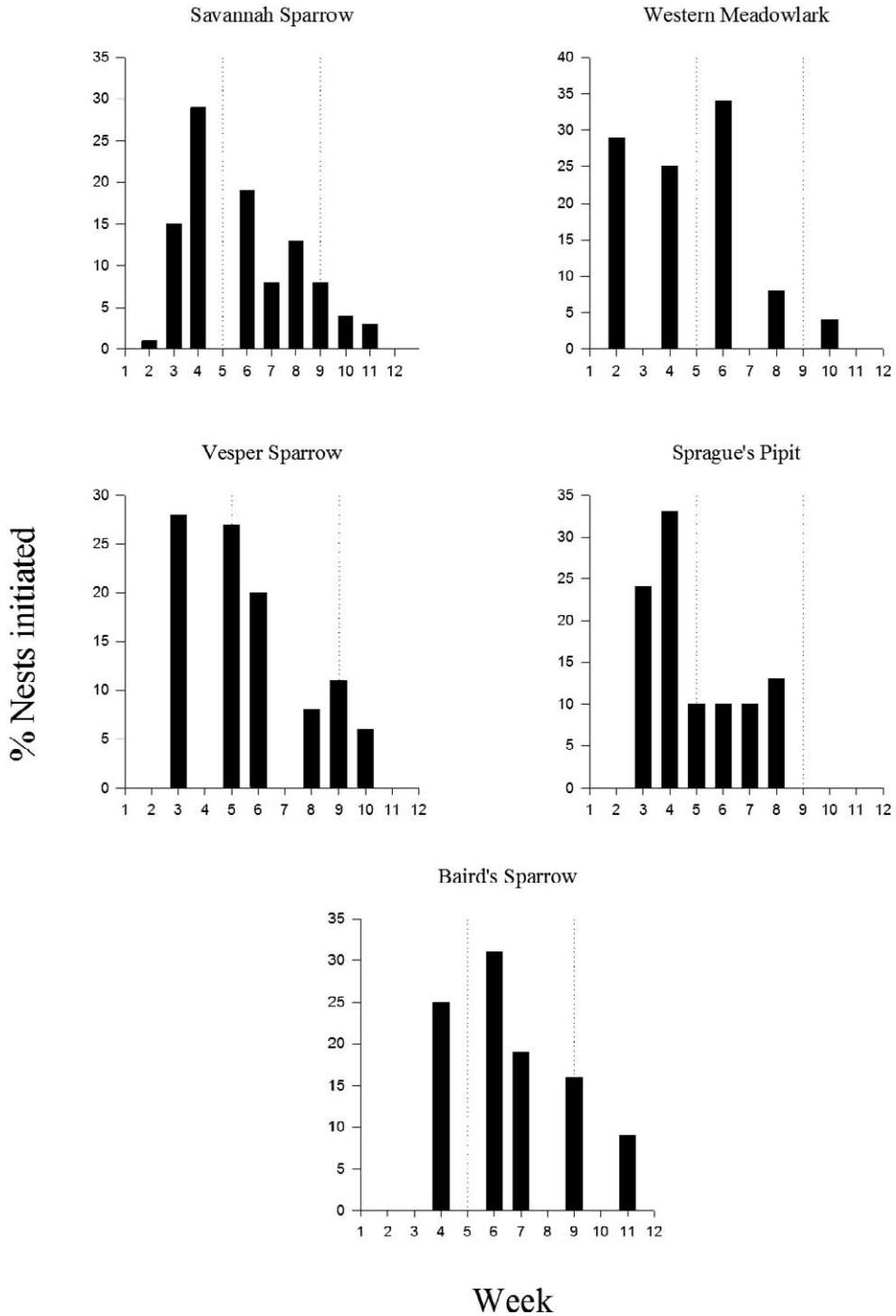
FIG. 1. Distribution of nests initiated over the breeding season for Savannah Sparrows, Vesper Sparrows, Baird's Sparrows, Western Meadowlarks, and Sprague's Pipits in southeast Alberta, 2010–2011. The breeding season is divided into weeks based on the following intervals: week 1 = May 1–7, week 2 = May 8–14, week 3 = May 15–21, week 4 = May 22–28, week 5 = May 29–June 4, week 6 = June 5–11, week 7 = June 12–18, week 8 = June 19–25, week 9 = June 26–July 2, week 10 = July 3–9, week 11 = July 10–16, and week 12 = July 17–23. Vertical dashed lines indicate the week in which 1 June and 1 July occur.

TABLE 1.   Clutch sizes of five grassland songbird species nesting in south-eastern Alberta, 2010–2011.

Species	Clutch size (%)						Mean ± SD
	2	3	4	5	6	7	
Sprague's Pipit (n = 21)	0	0	38	52	10	0	4.7 ± 0.6
Vesper Sparrow (n = 50)	2	22	66	10	0	0	3.8 ± 0.7
Savannah Sparrow (n = 166)	0	8	30	37	5	0	4.5 ± 0.9
Baird's Sparrow (n = 33)	0	12	36	49	3	0	4.4 ± 0.8
Western Meadowlark (n = 25)	0	4	12	28	52	4	5.4 ± 0.9

Meadowlarks remained relatively constant over the breeding season (-0.038 ± 0.05, 0.005 ± 0.09, and -0.047 ± 0.10, respectively).

Reproductive Success.—Of the nests we monitored, 29–52% of the nests successfully fledged host young (Table 2). The proportion of eggs laid that hatched ranged between 60–68% for all five species, and of the eggs incubated full term, 79–95% hatched (Table 2). Mean number of host young fledged per nest ranged from 0.8 for Vesper Sparrows to 1.9 for Sprague's Pipits, and the mean number of host young fledged per successful nest ranged from 2.9 for Vesper Sparrows to 4.6 for Western Meadowlarks (Table 2). Predation accounted for 75% of unsuccessful nests of all species, and Sprague's Pipits had the lowest apparent predation rates (Table 2).

Temporal factors best explained variation in nest survival for all species except Western Meadowlarks and Sprague's Pipits. A cubic effect of age was the top model explaining nest survival of Savannah and Vesper sparrows, and a quadratic effect of age was the top model explaining Baird's Sparrows' nest survival (Table 3, Appendix 1). Although model selection uncertainty was high, age was clearly the most influential variable as it was included in all top models (Table 3). Daily survival rates were highest during incubation, decreased at hatching, then increased through the nestling period for the three sparrow species (Fig. 2). We found no support for an effect of age or date on the nest survival of Sprague's Pipits and Western Meadowlarks. Nest survival did not differ between years for any of the five focal species, and there was no effect of date on nest survival as confidence limits overlapped zero in all cases.

Although temperature was included in the top model for Vesper Sparrows and precipitation was the top model for Sprague's Pipits (Table 4), confidence limits overlapped zero in both cases

TABLE 2.   Apparent nest success, hatching success, and productivity of five grassland songbirds in southeast Alberta, 2010–2011. Samples represent nests with known outcomes for each species. Failed nests represent nests that were unsuccessful because of reasons other than predation and desertion. Number of nests of each species is indicated after species name; the total number of eggs that hatched, and the number of eggs incubated full term are also provided.

Species	Sprague's Pipit (n = 21)	Vesper Sparrow (n = 52)	Savannah Sparrow (n = 189)	Baird's Sparrow (n = 35)	Western Meadowlark (n = 26)
% nests successful[a]	52	29	39	31	35
% nests depredated	29	54	47	51	46
% nests deserted	19	15	10	11	19
% nests failed	0	2	4	6	0
% eggs hatched (n)	61 (60)	68 (136)	68 (550)	68 (103)	60 (83)
% eggs incubated full term that hatched (n)	92 (65)	90 (151)	79 (641)	90 (115)	95 (87)
Host young fledged/nest	1.9 ± 2.0	0.8 ± 1.4	1.3 ± 1.9	1.1 ± 1.8	1.9 ± 2.4
Host young fledged/ successful nest	3.6 ± 1.1	2.9 ± 1.0	3.4 ± 1.5	3.6 ± 0.8	4.6 ± 0.7

[a] Fledged at least one host young.

TABLE 3. Model selection results for logistic exposure models of daily survival rate (DSR) on nest age and date for Savannah, Vesper, and Baird's sparrows in southeast Alberta, 2010–2011. Western Meadowlark and Sprague's Pipit are excluded because the null model was the top model. Log (L) is the value of the maximized log-likelihood function, K is the number of parameters in the model, AIC_c is Akaike's Information Criteria adjusted for small sample size, ΔAIC_c is the scaled value of AIC_c, and w_i is the Akaike weight. AGE represents the age of the nest, with zero being the day the first egg is laid. DATE represents the date at which the nest was active. NULL is constant survival regardless of age or date. Higher order terms include all lower order terms (e.g., AGE^3 includes AGE^2 and AGE). Only models that are within 3 ΔAIC of the best model are presented.

Model	Log (L)	K	ΔAIC_c	w_i
Vesper Sparrow				
AGE^3	−64.7	4	0.0	0.31
AGE^3 + DATE	−64.1	5	0.9	0.20
AGE^2	−66.7	3	2.1	0.11
AGE^3 + $DATE^2$	−63.9	6	2.7	0.08
AGE^2 + DATE	−66.0	4	2.7	0.08
AGE + DATE	−67.1	3	2.8	0.08
NULL	−77.8	1	23.4	0.00
Savannah Sparrow				
AGE^3	−247.0	4	0.0	0.57
AGE^3 + DATE	−246.7	5	1.4	0.29
AGE^3 + $DATE^2$	−246.4	6	2.8	0.14
NULL	−263.3	1	26.4	0.00
Baird's Sparrow				
AGE^2	−44.3	3	0.0	0.25
AGE^3	−43.6	4	0.5	0.19
AGE^2 + DATE	−44.0	4	1.3	0.13
AGE	−46.3	2	1.9	0.10
AGE^3 + DATE	−43.3	5	2.1	0.09
AGE + DATE	−45.4	3	2.1	0.09
NULL	−48.7	1	4.7	0.02

(Appendix 2). The quadratic effect of temperature was included in the top model for Baird's Sparrows' nest survival (Table 4, Appendix 2). We found no support for weather effects on nest survival for Savannah Sparrows or Western Meadowlarks (Table 4).

Nest visibility was lowest for Western Meadowlarks (0.5 ± 0.6 disc sections) and Sprague's Pipits (1.0 ± 0.6 disc sections) and highest for Vesper Sparrows (2.5 ± 1.8 disc sections); Savannah (1.7 ± 1.4 disc sections) and Baird's (1.3 ± 1.4 disc sections) sparrows had intermediate mean nest visibility values. Savannah Sparrows' nest survival decreased with increased nest visibility ($\beta \pm SE = -0.13 \pm 0.07$), but the relationship between nest visibility and nest survival was highly variable for Vesper Sparrows ($\beta \pm SE = 0.09 \pm 0.11$), Baird's Sparrows ($\beta \pm SE = 0.34 \pm 0.25$), Western Meadowlarks ($\beta \pm SE = 0.22 \pm 0.39$), and Sprague's Pipits ($\beta \pm SE = -0.59 \pm 0.66$).

Cowbird Parasitism.—Of the five species, Savannah Sparrow was the primary host for Brown-headed Cowbirds with ~11% of nests parasitized (Table 5). Savannah Sparrow was the only species to fledge cowbird young with 21% of cowbird eggs surviving to fledging (Table 5). Forty percent of parasitized Savannah Sparrows' nests and all parasitized Vesper Sparrows' nests contained more than one cowbird egg (Table 5). Parasitized Savannah Sparrows' nests had reduced reproductive rates compared to non-parasitized nests. Fewer eggs hatched from parasitized nests (1.6 ± 1.3) compared to non-parasitized nests (3.1 ± 1.9). Of those eggs incubated full term, 2.3 ± 1.6 eggs hatched from parasitized nests compared to 3.5 ± 2.0 eggs in non-parasitized nests. Fewer young fledged from parasitized nests (0.7 ± 1.0) than non-parasitized nests (1.4 ± 2.0). Out of successful nests, 1.9 ± 0.9 young fledged from parasitized nests compared to 3.6 ± 1.4 from non-parasitized nests. Clutch size was reduced in parasitized nests (3.0 ± 1.3) compared to non-parasitized nests (4.5 ± 0.8). Hatching and fledging success were similar for nests with one cowbird egg or young (1.4 ± 1.4 eggs and 0.6 ± 1.0 young, respectively) and those with multiple cowbird eggs or young (1.6 ± 1.3 eggs 0.7 ± 1.1 young, respectively). The number of host young fledged from successful unparasitized Savannah Sparrows' nests (3.6 ± 0.2) was approximately twice that of successful parasitized nests (1.9 ± 0.3). We found little evidence that predation rates differed between parasitized and non-parasitized Savannah Sparrows' nests ($P = 0.51$) or for all passerine species combined ($P = 0.73$).

DISCUSSION

Clutch Initiation and Clutch Size.—The simultaneous arrival of a large number of birds, followed by territory establishment and commencement of egg-laying, likely resulted in the early peak in clutch initiation observed at ACHDA. Arrival date has a strong influence on laying date, with earlier arriving birds initiating clutches sooner (Cristol 1995, Davis 2003). In general, mean clutch initiation dates corresponded with typical arrival times for the five focal species
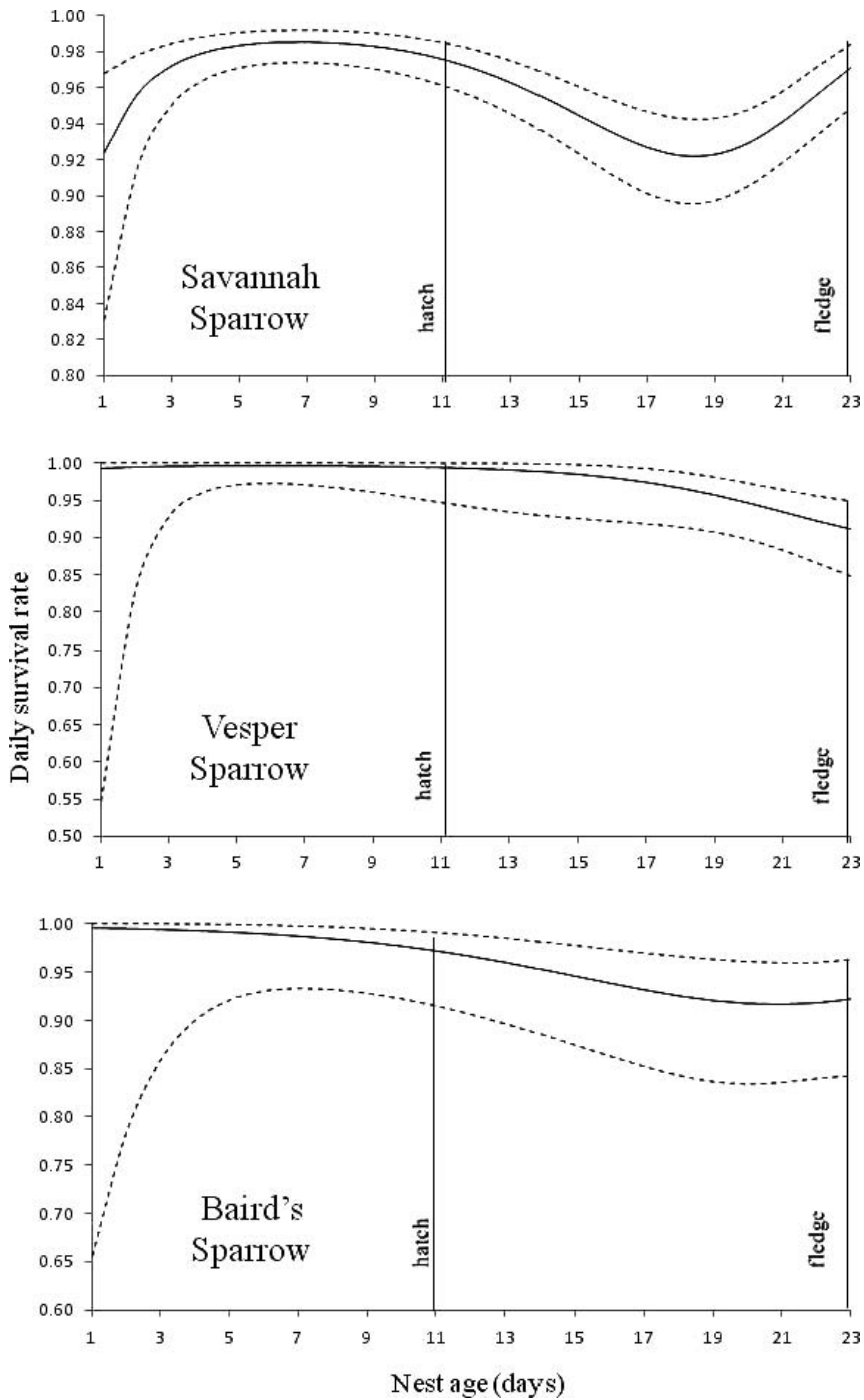
FIG. 2. Daily nest survival rate of Savannah Sparrows, Vesper Sparrows, and Baird's Sparrows in relation to nest age (days) in southeast Alberta, 2010–2011. Dashed lines indicate unconditional 95% confidence intervals for the logistic exposure model. Day 1 is the first day of incubation.

TABLE 4. Model selection results for the logistic exposure models of daily survival rate (DSR) as a function of weather for five species of grassland songbirds in southeast Alberta, 2010–2011. Models represent top temporal and weather models for each species as well as a global model combining the two and a null model. For species with no apparent age effects, the top three weather models are presented. TEMP and PPT represent the linear effect of temperature and precipitation, respectively. Higher order terms include all lower order terms (e.g., AGE^3 includes AGE^2 and AGE). Only species that had environmental or temporal models better than null are included.

Model	Log (L)	K	ΔAICc	w_i
Sprague's Pipit				
PPT	−20.6	2	0.0	0.32
NULL	−21.7	1	0.2	0.28
PPT + TEMP	−20.1	3	1.1	0.19
TEMP	−21.7	2	2.2	0.10
Vesper Sparrow				
AGE^3 + TEMP	−63.6	5	0.0	0.38
AGE^3	−64.8	4	0.4	0.31
AGE^3+PPT	−64.4	7	1.5	0.18
NULL	−77.8	1	20.3	0.00
Savannah Sparrow				
AGE^3	−247.0	4	0.0	0.74
AGE^3 + $TEMP^2$ + PPT	−245.1	7	2.1	0.26
$TEMP^2$ + PPT	−259.9	4	25.6	0.00
NULL	−263.4	1	26.8	0.00
Baird's Sparrow				
AGE^2 + $TEMP^2$	−40.7	5	0.0	0.76
AGE^2	−44.3	3	3.2	0.16
$TEMP^2$	−45.2	3	4.8	0.07
NULL	−48.7	1	7.9	0.01

and clutch initiation dates reported in other studies (Davis 2003, Jones et al. 2010). The synchronicity in egg-laying resulting in a slight increase in the number of nests initiated later in the breeding season may be the result of simultaneous nest failure because of adverse

weather and subsequent re-nesting. Indeed, we observed widespread nest failure following extreme weather events at ACHDA (SML, pers. obs.).

Clutch sizes fell within the range of previously reported values for all species in our study (Wray et al. 1982, George et al. 1992, Davis 2003, Jones et al. 2010) and tended to decrease as the breeding season progressed for Vesper and Baird's sparrows. A decrease in clutch size over the breeding season has been reported in many avian taxa (Perrins and McCleery 1989, Rowe et al. 1994), including grassland songbirds (Winter 1999, Davis 2003, Jones et al. 2010). The larger clutch sizes observed earlier in the breeding season at ACHDA may be because of decreased physical condition later in the season resulting from re-nesting and double brooding (Slagsvold 1982, Wray et al. 1982), or a larger diversity of prey taxa available to feed nestlings earlier in the season (Maher 1974).

Reproductive Success.—Predation was the primary cause of nest failure for all species; 75% of failed nests were lost to predators, 19% to desertion, and 5% to other causes such as inclement weather and cattle trampling. The frequency of nest predation at ACHDA is comparable to previously reported rates for grassland songbirds (Wray et al. 1982, Davis 2003, Jones et al. 2010). Hatching success was at least 5% higher at ACHDA than south-central Saskatchewan (Davis 2003) for Savannah Sparrows, Baird's Sparrows, Western Meadowlarks, and Sprague's Pipits but 10–24% lower than Montana (Jones et al. 2010). The mean number of young fledged per nest and per successful nest of Savannah Sparrows, Baird's Sparrows, and Sprague's Pipits was similar at ACHDA to previously reported values for these species in other parts of their range (Davis and Sealy 1998, Davis 2003,

TABLE 5. Frequency and intensity of cowbird parasitism and cowbird reproductive success in nests of five grassland songbird host species in southeast Alberta, 2010–2011.

Species (n)	% nests parasitized	% multiple parasitism	Mean (±SE) cowbird eggs laid	% cowbirds fledged (cowbird eggs)	Mean (±SE) cowbirds fledged / parasitized nest	Mean (±SE) cowbirds fledged/ successful parasitized nest[a]
Sprague's Pipit (n = 21)	0	0	0	0	0	0
Vesper Sparrow (n = 53)	2	100	2	0 (2)	0	0
Savannah Sparrow (n = 190)	11	5	1.7 ± 0.2	21 (33)	0.4 ± 0.1	0.9 ± 0.2
Baird's Sparrow (n = 35)	6	0	1.0 ± 0.2	0 (2)	0	0
Western Meadowlark (n = 26)	4	0	1	0 (1)	0	0

[a] Fledged at least one host or cowbird young.

Jones et al. 2010). Mean number of young fledged per nest was similar to previously reported values for Western Meadowlarks (Davis 2003, Jones et al. 2010); however, successful nests of Western Meadowlarks at ACHDA fledged ~0.7 more young than successful nests in Saskatchewan (Davis 2003) and Montana (Jones et al 2010). For Vesper Sparrows, the mean number of young fledged per nest and per successful nest at ACHDA was similar to values reported for this species on reclaimed surface mines in West Virginia (Wray et al. 1982) and native pastures in North Dakota (George et al. 1992). Hatching success of Vesper Sparrows at ACHDA was also similar to values reported in North Dakota (George et al. 1992). Based on the similar rates of hatching and fledging success in different locations and habitats, Vesper Sparrows appear to not only occupy a variety of disturbed grassland habitats but reproduce successfully there as well.

Nest survival peaked during mid-incubation, declined after hatching, then increased again late in the nestling stage for Savannah and Vesper sparrows and is consistent with data from elsewhere (Davis 2005, Grant et al. 2005, Kerns et al. 2010, Grant and Shaffer 2012). Baird's Sparrows' nest survival was greatest at the start of incubation then declined in the early nestling period before increasing just prior to fledging. Declining nest survival during incubation and early in the nestling period may be because of longer risk exposure (Grant et al. 2005). The longer a nest persists, the greater the likelihood of detection of the nest by predators. Declining survival early in the nestling period may also be because of increased parental activity. Parental activity is greater during the nestling stage than incubation (Roper and Goldstein 1997), potentially increasing the risk of nest predation during this stage (Martin et al. 2000, Muchai and du Plessis 2005). Higher predation rates during the nestling stage than during incubation have been found in songbirds nesting in forest (Cox et al. 2012), shrub (Thompson et al. 1999, Burhans et al. 2002), and grassland habitats (Pietz and Granfors 2000, Davis et al. 2012). In addition to increased parental activity, factors such as movement, noise, and olfactory cues from nestlings could attract predators to a nest (Petit et al. 1989, Briskie et al. 1999). Nests containing nestlings are more profitable for predators than nests containing eggs because of the larger mass of chicks, particularly older nestlings. However, the relevance of these factors to the rate of nest predation in a particular area is determined by composition of the local predator community (Roper and Goldstein 1997) and how the dominant predators locate nests (Herzog and Burghardt 1974, Eichholz and Koenig 1992).

Increasing nest survival from early to late in the nestling stage may result from a number of factors (Grant et al. 2005), such as reduced involuntary movements by nestlings and increased control over begging with increasing nestling age (Dawson and Evans 1957, Dawson and Evans 1960), increased thermoregulatory and self-defense capabilities of the young with age (Dawson and Evans 1957, Halupka 1998), and increased parental defense (Montgomerie and Weatherhead 1988, Tryjanowski and Goławski 2004). We did not find any effects of nest age on nest survival of Sprague's Pipits or Western Meadowlarks. Davis (2005) found that Sprague's Pipits' nest survival decreased with nest age and that Western Meadowlarks' nest survival was lowest shortly after hatching. A linear effect of age was the second-ranked model for nest survival of both Sprague's Pipits and Western Meadowlarks in this study, but the relatively small number of nests may have precluded us from detecting strong age-effects.

Baird's Sparrow was the only species whose nest survival was influenced by weather. Baird's Sparrows' nest survival was high at low (~4 °C) temperatures, decreased as temperatures increased to intermediate levels (~15 °C), then increased as temperatures increased (up to ~25 °C). Increased nest survival at high and low temperatures and reduced nest survival at intermediate temperatures may be because the incubating bird is more likely to be on the nest during temperature extremes but leaves the nest more frequently or for longer periods during intermediate temperatures (Davis and Holmes 2012, Kirkham and Davis 2013) thereby increasing predation risk during these times (Duncan Rastogi et al. 2006).

Nest concealment only influenced nest survival of Savannah Sparrows with survival increasing with more concealed nests. Nest concealment can have an important influence on nest predation (Martin 1993), but the latter is not always correlated with concealment because of variation in the predator community (Dion et al. 2000) or compensatory behaviors by parents (Remeš 2005). The variable relationship between nest survival and concealment among Vesper Sparrows, Baird's Sparrows, Western Meadowlarks,

and Sprague's Pipits may be because of small sample sizes or may reflect the diversity of the local predator community and the various ways different types of predators locate nests.

Cowbird Parasitism.—All species were parasitized by Brown-headed Cowbirds except Sprague's Pipit, and the rates of cowbird parasitism we observed in this study are similar to that in other regions of the northern mixed-grass prairie (Maher 1973, Jones et al. 2010, Gaudet 2013). Savannah Sparrows' nests were parasitized at least twice as frequently as the other host species. The lack of cowbird parasitism we found on Sprague's Pipits' nests corresponds with low levels of parasitism found by others (Davis and Sealy 2000, Davis 2003, Jones et al. 2010). The greater frequency of parasitism in Savannah Sparrows' nests may be because of the abundance of this species relative to the others; Savannah Sparrows' territory density at ACHDA was ~10 × that of the other four species (Ludlow 2013). Davis and Sealy (2000) found that the most abundant host species were also the most frequently parasitized on two of three study sites in southwestern Manitoba. Previous studies have shown that brood parasitism rates can be influenced by the regional abundance of hosts and cowbirds (Hoover and Brittingham 1993, Barber and Martin 1997). Savannah Sparrows may be selected by cowbirds, because they are better quality hosts than the other study species. Savannah Sparrows' eggs are similar in appearance to cowbird eggs (Klippenstine and Sealy 2010). Female Savannah Sparrows accept cowbird eggs (Klippenstine and Sealy 2008), and the species was the only one to successfully rear cowbird young in our study. Similarly, Savannah Sparrows in southwest Manitoba fledged proportionally more cowbird young than any of the other seven species examined (Davis and Sealy 2000). The frequency of cowbird parasitism in Savannah Sparrows' nests we found is similar to the frequency reported in Montana (Jones et al. 2010) but lower than Saskatchewan (Davis 2003), Manitoba (Davis and Sealy 2000), and North Dakota (Kerns et al. 2010). The frequency of cowbird young fledged from Savannah Sparrows' nests was lower than in Manitoba (Davis and Sealy 2000) but almost twice as high as in Saskatchewan (Davis 2003).

Brood parasitism is costly to hosts because of reduced reproductive success (Hoover 2003). Parasitized Savannah Sparrows' nests experienced reduced clutch size and lowered hatching and fledging success compared to non-parasitized nests. Reduced clutch size likely resulted from female cowbirds removing at least one host egg before laying one of their own (Sealy 1992). The presence of cowbird eggs or nestlings may reduce the hatching success of host eggs through egg capping (Hauber 2003a), reduced incubation efficiency, and disruption of host incubation patterns (Hauber 2003b). Cowbird parasitism can reduce fledging rates of the host clutch if the cowbird nestling out-competes its host nest-mates for food (Dearborn 1998). Cowbird parasitism cost Savannah Sparrows 1.7 young per successful nest. Similar estimates of the cost of cowbird parasitism have been reported for Savannah Sparrows in Manitoba (Davis 1994, Davis and Sealy 2000). Predation rates were similar for parasitized and non-parasitized nests, indicating that the presence of cowbird young did not substantially increase predation risk (Dearborn 1999), and any decrease in host productivity resulted from cowbird parasitism. Although pitfalls exist when comparing nest success between parasitized and non-parasitized nests (Zanette et al. 2007), such comparisons provide valuable information about the costs to hosts associated with cowbird parasitism during the nesting stage and represent the minimum of the potential costs to host reproduction associated with cowbird parasitism (Rasmussen and Sealy 2006).

Nest predation was the most important factor influencing the reproductive success of grassland songbirds in southeast Alberta. High rates of nest predation are common in other studies of grassland songbirds at other locations (Davis 2005, Jones et al. 2010). Brood parasitism was also an important factor influencing reproductive success of Savannah Sparrows; however, parasitism rates varied with those found in other locations, suggesting that the impact of brood parasitism on host reproductive success varies geographically within a species range. Furthermore, to fully understand the effects of predation and brood parasitism on reproductive success additional demographic parameters need to be addressed, such as adult and fledgling survival and the tendency of a species to re-nest and raise multiple broods.

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APPENDIX 1.   Model averaged parameter estimates for temporal models of Savannah Sparrows, Vesper Sparrows, and Baird's Sparrows in southeast Alberta, 2010–2011. Model averaged results for Western Meadowlarks and Sprague's Pipits are not presented, because the null model was the top model. AGE represents the age of the nest, and DATE represents the date at which the nest was active. Higher order terms include all lower order terms (e.g., AGE^3 includes AGE^2 and AGE).

Parameter	Estimate	Standard error	Lower 85% CI	Upper 85% CI
Vesper Sparrow				
Intercept	−2.0255	11.5518	−18.66	14.6091
AGE	1.4356	2.1341	−1.6376	4.5087
AGE^2	−0.0753	0.1115	−0.2358	0.0852
AGE^3	0.0017	0.0008	0.0005	0.0028
DATE	0.0558	0.1720	−0.1918	0.3035
$DATE^2$	−0.0001	0.0216	−0.0312	0.0310
Savannah Sparrow				
Intercept	−2.7685	6.9134	−12.724	7.1868
AGE	1.8641	1.9093	−0.8854	4.6136
AGE^2	−0.1196	0.1245	−0.2989	0.0597
AGE^3	0.0023	0.0005	0.0015	0.003
DATE	−0.0215	0.0355	−0.0726	0.0297
$DATE^2$	0.0001	0.0003	−0.0003	0.0004
Baird's Sparrow				
Intercept	6.6092	11.8077	−10.394	23.6123
AGE	0.0205	0.9041	−1.2814	1.3224
AGE^2	−0.0636	0.1104	−0.2225	0.0953
AGE^3	0.0014	0.001	−0.0001	0.0029
DATE	0.0154	0.0174	−0.0097	0.0405

APPENDIX 2. Parameter estimates for the best logistic exposure model explaining the effects of weather and age on daily survival rates for five species of grassland songbirds in southeast Alberta, 2010–2011. Only species that had environmental or temporal models better than null are included. AGE represents the age of the nest, TEMP represents ambient temperature, and PPT represents precipitation. Higher order terms include all lower order terms (e.g., AGE^3 includes AGE^2 and AGE).

Parameter	Estimate	Odds ratio	Lower 85% CI	Upper 85% CI
Sprague's Pipit				
Intercept	3.363	28.876	2.595	4.270
PPT	0.266	1.305	−0.081	0.081
Vesper Sparrow				
Intercept	−6.145	0.002	−17.688	0.003
AGE	2.280	9.777	0.240	0.003
AGE^2	−0.153	0.858	−0.265	−0.145
AGE^3	0.003	1.003	0.001	1.765
TEMP	0.132	1.141	0.008	−0.304
Baird's Sparrow				
Intercept	25.072	7.70E+10	9.625	40.519
AGE	−0.532	0.587	−1.049	−5.014
AGE^2	0.010	1.010	−0.002	0.079
TEMP	−2.262	0.104	−4.185	−1.152
$TEMP^2$	0.080	1.083	0.017	0.022