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NESTING ECOLOGY OF MIXED-GRASS PRAIRIE SONGBIRDS IN SOUTHERN SASKATCHEWAN

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ABSTRACT.—During 1996–2000, I studied the nesting ecology of Sprague's Pipits (*Anthus spragueii*), Clay-colored Sparrows (*Spizella pallida*), Savannah Sparrows (*Passerculus sandwichensis*), Baird's Sparrows (*Ammodramus bairdii*), Chestnut-collared Longspurs (*Calcarius ornatus*), and Western Meadowlarks (*Sturnella neglecta*) on 47 native mixed-grass prairie pastures in southern Saskatchewan. Predation was the primary cause of nest failure and occurred at a similar frequency among the six species. Nest success and productivity varied among years and was lowest during 1997, the year of a substantial increase in meadow vole (*Microtus pennsylvanicus*) populations in southern Saskatchewan. Nest predation was most severe during the nestling stage with daily survival rates typically lower than those of the incubation period. Brown-headed Cowbirds (*Molothrus ater*) parasitized nests of all six species, with 5–29% of host nests containing cowbird eggs. Savannah Sparrows, Clay-colored Sparrows, and Western Meadowlarks incurred the highest frequency of brood parasitism. Parasitized hosts experienced lower productivity due to a combination of reductions in clutch size, hatching success, and fledging success. Overall, brood parasitism by cowbirds cost these birds between 1.3 and 2.2 young per successful nest. These results support the general contention that nest predation is the primary factor influencing grassland songbird reproductive success. *Received 10 December 2002, accepted 12 March 2003.*

The nesting ecology of grassland songbirds in the northern mixed-grass prairie has received little attention, partly because of the perceived and real difficulty in locating nests (Bent 1950, Lane 1968). Subsequently, our ability to adequately identify proximate and ultimate factors contributing to the widespread population declines of grassland birds (Sauer et al. 2001) often is limited because we lack basic information on many aspects of their breeding ecology, particularly factors influencing their reproductive success. Sprague's Pipit (*Anthus spragueii*), for example, is listed as a threatened species (Committee on the Status of Endangered Wildlife in Canada 2000), and has been described as one of North America's least-known birds (Robbins and Dale 1999). Although several recent studies have examined habitat use in northern grassland songbirds (Dale et al. 1997, Sutter and Brigham 1998, Davis et al. 1999, Madden et al. 2000, Johnson and Igl 2001, McMaster and Davis 2001), only Maher (1973), Koford (1999), and Davis and Sealy (2000) have reported on aspects of the breeding biology and factors reducing nest success of this songbird community. Other studies in the northern Great Plains have involved single species (Knapton 1978, Hill 1997, Davis and Sealy 1998), or have focused on only brood parasitism (Koford et al. 2000), making demographic comparisons within and among grassland bird communities difficult.

Nest predation and brood parasitism often are cited as the primary factors responsible for lowering reproductive success of grassland songbirds. Martin (1993) showed that grassland species typically experience higher rates of nest predation than birds nesting in forest and wetland habitats. Although nest success varies regionally, recent studies indicate that as many as 70% of grassland bird nests are destroyed by predators (Patterson and Best 1996, Best et al. 1997, Winter 1999, Davis and Sealy 2000). Brown-headed Cowbirds (*Molothrus ater*) also may lower reproductive success by removing host eggs and out competing host nestlings for food and space (Payne 1977). However, as with nest predation, the frequency and impact of brood parasitism on grassland hosts vary geographically. Robinson et al. (2000) found that grassland hosts in Illinois experienced parasitism frequencies of <5%, whereas parasitism frequencies in other regions often were >30% (Koford et al. 2000). In this paper I quantify the extent of nest predation and brood parasitism and compare aspects of the nesting ecology of six grassland songbirds in native

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mixed-grass prairie pastures in southern Saskatchewan, Canada.

METHODS

Study area.—I conducted the study on native pastures in the eastern portion of the mixed- and moist mixed-grassland ecoregions of southern Saskatchewan (49° 45′ N, 105° 45′ W; see Davis et al. 1999 for a description of the region) during the 1996–2000 nesting seasons. I selected pastures in fair-to-good range condition under light-to-moderate grazing intensity (Task Group on Unity in Concepts and Terminology 1995) to increase the likelihood of locating nests of high conservation priority species such as Baird's Sparrow (*Ammodramus bairdii*) and Sprague's Pipit, and to ensure similar breeding bird communities among sites. A different set of pastures was selected for most years of the study for a total of 47 pastures on which nests were located (8 pastures during 1996, 12 during 1997, 10 each during 1998 and 1999, and 7 during 2000). Native pastures were flat to gently rolling and the vegetation consisted predominantly of *Stipa* spp., June grass (*Koeleria macrantha*), northern wheatgrass (*Elymus lanceolatus*), western wheatgrass (*Pascopyrum smithii*), blue grama (*Bouteloua gracilis*), sedges (*Carex* spp.), club moss (*Selaginella densa*), sage (*Artemisia* spp.), and various other forbs. Common shrubs were western snowberry (*Symphoricarpos occidentalis*) and rose (*Rosa* spp.).

Nest searches.—Nest searching and monitoring were conducted from early May to early August each year. Nests were located mostly between 07:30 and 14:00 CST by flushing adults from their nests with a 25-m nylon rope weighted with aluminium and tin cans attached every 0.5 m. Nests also were located fortuitously on the pastures throughout the day. Nests were marked with color surveyor flags and bamboo stakes placed 5 m away and monitored every 2–5 days until the young fledged or the nesting attempt failed. Eggs were candled (Lokemoen and Koford 1996) to determine clutch initiation dates and to estimate hatching dates for increased accuracy in calculating survival rates (Mayfield 1975). Nest attempts were considered successful if at least one host nestling survived to fledging age (i.e., left the nest), except when comparing parasitized and nonparasitized nests for which successful nests included nests fledging at least one host or cowbird young. Cues such as adult(s) uttering alarm calls nearby, nestling age on previous visit, minimal nest disturbance, fledglings in the vicinity of the nest, and the presence of feces and feather scales in the nest were used to identify successful nests.

Statistical analyses.—I conducted all analyses using SAS ver. 8 (SAS Institute, Inc. 1999). I used the median test (PROC NPAR1WAY) to determine whether median clutch initiation dates differed among years for each species. Clutch initiation dates from 1996 were not included in this analysis, as eggs were not candled during that year. To determine whether host clutch size changed as the breeding season progressed, I calculated the mean clutch size during each week and regressed the mean clutch size as a function of week using the square root of the number of nests as a weighting factor. Weekly periods that comprised only one nest were excluded from analyses. I calculated daily survival rates using the Mayfield method (Mayfield 1961, 1975) with standard errors as per Johnson (1979). I used only the incubation and nestling periods to calculate nest success. The halfway point between the last visit when the nest was active and a subsequent visit was used to calculate the number of exposure days for nests with known fate. For nests whose fates were uncertain, I included exposure days only up to the last visit that the nest was active (Manolis et al. 2000). I compared daily survival rates during the incubation and nestling periods using Johnson's (1979) methodology. I used one-way ANOVA and least squares means, weighted by the square root of exposure days for each year, to determine whether daily survival rates differed among years. I used pastures as sample units to avoid pseudoreplication (Hurlbert 1984) as individual nests within a pasture likely are not independent. I used the same analyses to determine whether productivity differed among years, except that I used the square root of the number of nests as a weighting factor. I compared clutch size, hatching success, and productivity of parasitized and nonparasitized nests using Student's *t*-tests (PROC TTEST).

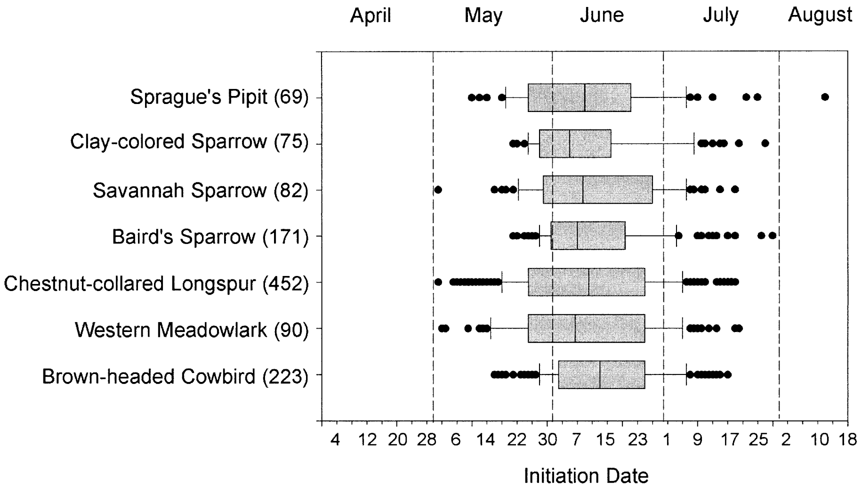

FIG. 1. Peak egg laying occurred during the first two weeks of June for grassland songbirds in southern Saskatchewan, 1997–2000. Number of nests or cowbird eggs are in parentheses. Box plots represent 25th, 50th, and 75th percentiles; whiskers indicate 10th and 90th percentiles; and dots are outliers.

RESULTS AND DISCUSSION

Overall, 1,300 nests of 27 species were located over the five years of the study. Most nests were passerines (n = 1,083), followed by waterfowl (n = 150), shorebirds (n = 59), and grouse (n = 5), along with two Common Nighthawk (*Chordeiles minor*) nests and one Short-eared Owl (*Asio flammeus*) nest. This paper focuses on the six songbird species that composed 80% of the total number of nests: Chestnut-collared Longspur (*Calcarius ornatus*, n = 500), Baird's Sparrow (n = 184), Western Meadowlark (*Sturnella neglecta*, n = 111), Savannah Sparrow (*Passerculus sandwichensis*, n = 88), Clay-colored Sparrow (*Spizella pallida*, n = 85), and Sprague's Pipit (n = 67).

Clutch initiation.—The peak of clutch initiation occurred within the first two weeks of June for most songbirds (Fig. 1). Western Meadowlarks and Chestnut-collared Longspurs typically initiated nests earlier, and Baird's and Clay-colored sparrows nested later in the breeding season. Initiation dates are consistent with typical arrival times of these species. During 1995–2002 in Saskatchewan, Western Meadowlarks and Chestnut-collared Longspurs usually arrived during the first and third weeks of April, respectively, whereas Baird's and Clay-colored sparrows arrived during the first two weeks of May (unpubl. data). Savannah Sparrows and Sprague's Pipits typically arrived in late April to early May. Davis (1994) found a similar pattern in the breeding phenology of grassland birds in southwestern Manitoba. Median clutch initiation dates differed significantly among years for Chestnut-collared Longspurs (χ^2 = 21.49, df = 3, $P < 0.0001$) and Western Meadowlarks (χ^2 = 8.19, df = 3, P = 0.042) and tended to differ among years for Sprague's Pipits (χ^2 = 6.68, df = 3, P = 0.080). Longspurs and pipits initiated nests later in 1997 than in subsequent years, whereas meadowlarks initiated nests earlier in 1997 and 1999 than in other years. Longspurs arrived a week later in 1997 (5 May) compared to 1996 (28 April) and more than two weeks later than in 1998–2000 (17–19 April). The variation in laying phenology of pipits and meadowlarks, however, did not appear to be influenced by arrival dates, as arrival dates were similar for all years.

Clutch size.—Clutch sizes of all species (Table 1) fell within the range of those reported previously (Wheelright and Rising 1993, Knapton 1994, Lanyon 1994, Sutter 1996, Hill and Gould 1997, Davis and Sealy 1998). Baird's Sparrows, Savannah Sparrows, and Sprague's Pipits typically laid four or five eggs whereas Clay-colored Sparrows and Chestnut-collared Longspurs mostly laid four-egg clutches. Five- and six-egg clutches were most commonly observed in Western Mead-

TABLE 1. Clutch sizes of six grassland songbirds nesting in southern Saskatchewan, 1996–2000.

Species	Clutch size (%) 2	3	4	5	6	Mean ± SE
Sprague's Pipit ($n = 57$)	1 (1.7)	1 (1.7)	18 (31.6)	26 (45.7)	11 (19.3)	4.8 ± 0.11
Clay-colored Sparrow ($n = 57$)	0	10 (17.5)	46 (80.7)	1 (1.8)	0	3.8 ± 0.05
Savannah Sparrow ($n = 61$)	1 (1.6)	3 (5.0)	28 (45.9)	28 (45.9)	1 (1.6)	4.4 ± 0.09
Baird's Sparrow ($n = 146$)	0	6 (4.1)	52 (35.6)	88 (60.3)	0	4.6 ± 0.05
Chestnut-collared Longspur ($n = 414$)	7 (1.7)	52 (12.6)	227 (54.8)	122 (29.5)	6 (1.4)	4.2 ± 0.03
Western Meadowlark ($n = 73$)	0	5 (6.8)	10 (13.7)	33 (45.2)	25 (34.3)	5.1 ± 0.10

owlark nests. A quadratic relationship best described Baird's Sparrow and Chestnut-collared Longspur clutch size as a function of week whereas Western Meadowlark clutch size decreased as the breeding season progressed (Fig. 2). Savannah Sparrow clutch size tended to decrease with the breeding season ($t = -2.14$, df = 8, $P = 0.069$) while Sprague's Pipit clutches tended to be largest midway through the breeding season ($F_{2,6} = 3.76$, $P = 0.087$). Clutch size of Clay-colored Sparrows did not vary significantly as the breeding season progressed ($F_{2,4} = 0.93$, $P = 0.46$). Previous studies have reported decreasing clutch sizes during the breeding season for Western Meadowlarks and Savannah Sparrows (Lanyon 1957, Dixon 1978, Wray et al. 1982), although Dickinson et al. (1987) found only a weak relationship for meadowlarks. Maher's (1973) observations that Sprague's Pipit and Chestnut-collared Longspur clutches initiated in June tended to be larger than those initiated in May or July are consistent with my results. Davis and Sealy (1998) found that Baird's Sparrows typically laid larger clutches earlier in the breeding season. Smaller clutches earlier in the season for some species may reflect lower metabolic resources due to energetic demands during migration and lower prey abundance during early summer, whereas reduced metabolic resources later in the season may result from renesting and double brooding (Wray et al. 1982).

Nest success and productivity.—Nest predation was the major cause of reproductive failure, with nest desertion and other causes of nest failure accounting for a small proportion of unsuccessful nests (Table 2). Overall, predation accounted for 88% of unsuccessful nests, which is comparable to rates reported for grassland songbirds in other regions (Wray et al. 1982, Davis 1994, Knapton 1994, Hill and Gould 1997, Winter 1999, S. L. Jones unpubl. data). Apparent nest success, predation, and productivity were similar among species, although Clay-colored Sparrows were least successful, due to a combination of higher frequencies of desertion and nest failure unrelated to predation (i.e., inclement weather and cattle activity). Hatching success for the six species ranged between 55 and 63%, and of the eggs incubated full term, 65–77% hatched (Table 2).

Daily survival rates were higher during the incubation period than during the nestling period for all species, although differences were not significant ($P > 0.10$ in all cases). S. L. Jones (unpubl. data) found that survival was higher during the incubation stage for six of seven grassland songbird species studied in Montana, and Davis (1994) found a similar pattern for four of six species in Manitoba. Patterson and Best (1996) also reported higher survival rates during the incubation period for four of five species breeding in Iowa, whereas Winter (1999) found that survival of Dickcissel (*Spiza americana*) nests in Missouri was lower during the incubation period and found no difference in egg and nestling survival in Henslow's Sparrows (*Ammodramus henslowii*). The lower survival rates during the nestling period may be due to predators cuing in on the increased activity of adults feeding young and nestlings begging for food (Haskell 1994), although this likely depends upon the composition of the predator community (i.e., predators relying primarily on visual instead of auditory cues) and parental behavior (Halupka 1998).

Mayfield nest success ranged from 13.9% for Clay-colored Sparrows to 24.0% for Sprague's Pipits (Table 3). Davis and Sealy

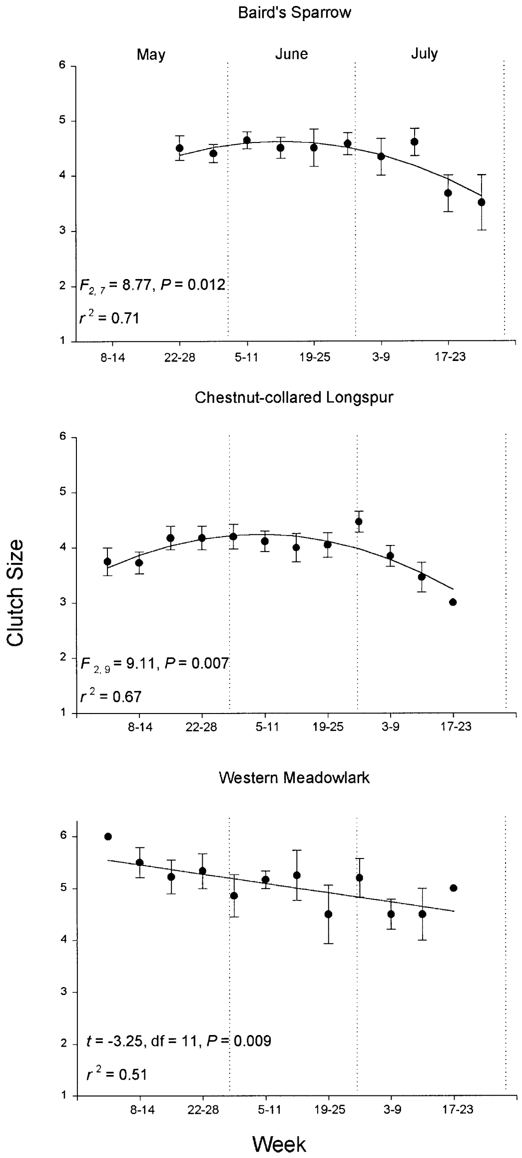

FIG. 2. Clutch size varied with breeding season for three grassland songbirds in southern Saskatchewan, 1997–2000. Values are means ±SE.

(2000) reported lower nest success rates for most species in a similar bird community in southwestern Manitoba, although nest success for Chestnut-collared Longspurs in Manitoba was higher (30%) compared to Saskatchewan (21.6%). Similarly, in Montana, nest success rates were 4–11% higher for similar species over the same period (S. L. Jones unpubl. data). The low success rates I observed were due mainly to poor nest success during 1997 (Fig. 3), particularly for Sprague's Pipits ($F_{3,18} = 7.39$, $P = 0.002$) and Baird's Sparrows ($F_{4,31} = 6.04$, $P = 0.001$). This likely was related to a substantial increase in meadow vole (*Microtus pennsylvanicus*) populations that occurred over a large region of southern Saskatchewan (Poulin et al. 2001), whereas no such phenomenon occurred in Montana (S. L. Jones pers. comm.). With the 1997 data removed, nest success estimates increased to 24–32%, which is comparable to those found in Montana. Interestingly, the low nest success during 1997 may be attributed mainly to lower survival during the nestling stage. Daily survival rates during the incubation period did not differ significantly among years ($P > 0.25$), whereas nestling daily survival rates differed among years for Savannah Sparrows ($F_{4,20} = 2.70$, $P = 0.060$) and Sprague's Pipits ($F_{3,17} = 13.06$, $P = 0.0001$); nestling daily survival rates were lowest during 1997 and 1998 for Savannah Sparrows and lowest during 1997 for Sprague's Pipits. Temporal variation in nest predation has been linked to vole populations in other regions. Bientema and Muskens (1987), for example, found that nest success of shorebirds was related to the amount and direction of changes in vole densities. Nest predators appeared to shift to bird nests following a collapse in vole populations. Although nest success of large birds may be relatively high during years when voles are abundant because predators switch from bird nests to voles, voles may lower nest success of songbirds directly by depredating their nests (Bures 1997). It is unknown whether voles were directly responsible for increased nestling mortality in this study or whether the increased mortality was due to higher rates of incidental predation resulting from increased number of predators responding to the voles.

The low nest success during 1997 resulted in relatively low productivity for Baird's Sparrows ($F_{4,39} = 3.23$, $P = 0.022$), Sprague's Pipits ($F_{3,23} = 5.36$, $P = 0.006$), and Western Meadowlarks ($F_{4,36} = 3.16$, $P = 0.025$; Fig. 4). The mean number of host young fledged by Baird's Sparrows was lower during 1997 and 1998 than during 1999 or 2000, and the productivity of pipits was highest during 1999. Meadowlarks fledged significantly more young in 1996 than during 1997–1999. The

TABLE 2. Apparent nest success, hatching success, and productivity of six grassland birds in southern Saskatchewan, 1996–2000. Sample sizes represent the number of nests with known outcomes for each species.

Species	Sprague's Pipit ($n = 65$)	Clay-colored Sparrow ($n = 79$)	Savannah Sparrow ($n = 80$)	Baird's Sparrow ($n = 167$)	Chestnut-collared Longspur ($n = 474$)	Western Meadowlark ($n = 95$)
Percentage of nests successful[a]	30.8	20.3	27.5	25.8	29.5	29.5
Percentage of nests depredated	55.4	60.8	61.3	62.9	64.4	64.2
Percentage of nests deserted	9.2	8.9	3.8	5.4	1.7	1.0
Percentage of nests failed	4.6	10.1	7.5	6.0	4.4	5.3
Percentage of eggs hatched (n)	55.1 (55)	61.6 (53)	63.0 (55)	59.5 (132)	58.9 (390)	55.1 (65)
Percentage of eggs incubated full term that hatched (n)	64.9 (46)	71.4 (45)	76.9 (45)	75.4 (103)	76.6 (299)	68.5 (52)
Host young fledged/nest	1.0 ± 0.22	0.6 ± 0.14	0.8 ± 0.17	0.9 ± 0.13	0.9 ± 0.07	1.0 ± 0.17
Host young fledged/successful nest (n)	3.4 ± 0.32 (20)	3.0 ± 0.24 (16)	3.0 ± 0.26 (22)	3.4 ± 0.19 (43)	3.0 ± 0.10 (141)	3.4 ± 0.22 (29)

[a] Fledged at least one host young.

number of young fledged per successful nest varied among years for Baird's Sparrow and Western Meadowlark ($F_{4,21} = 2.47$, $P = 0.076$ and $F_{4,17} = 4.53$, $P = 0.011$, respectively; Fig. 4). Baird's Sparrow nests fledged more young from successful nests during 1999 than 1996 or 1997, and Western Meadowlarks fledged the fewest young in 1997.

Overall, grassland songbirds in Saskatchewan fledged between 0.6 and 1.0 young per nest and between 3.0 and 3.4 young from successful nests (Table 2). As with nest success, S. L. Jones (unpubl. data) reported higher fledging rates in Montana (1.2–1.7 host young/nest), but the number of host young fledged from successful nests (2.9–3.5) was similar to what I observed.

Cowbird parasitism.—The median egg-laying dates for Brown-headed Cowbirds did not differ significantly among years ($\chi^2 = 4.43$, df = 3, $P = 0.22$). Overall, the cowbird egg-laying season extended from 16 May to 17 July and peaked during the second week of June. Although some host nests were initiated before or after the cowbird laying season, most nests were available to cowbirds throughout the breeding season (Fig. 2). Parasitism frequency varied among years for Chestnut-collared Longspurs ($\chi^2 = 44.31$, df = 4, $P < 0.0001$), Savannah Sparrows (Fisher's Exact Test, $P = 0.053$), and Western Meadowlarks (Fisher's Exact Test, $P = 0.001$). Longspurs were parasitized more frequently during 1996 (50%) than during subsequent years (9–18%), whereas Savannah Sparrows and Western Meadowlarks were parasitized most frequently during 1996 (40 and 50%, respectively) and 1997 (45 and

TABLE 3. Mayfield nest success and daily survival rates (DSR ± SE) for incubation and nestling periods of six grassland songbirds in southern Saskatchewan, 1996–2000.

Species	Incubation period (days)	Nestling period (days)	Number of nests	Incubation DSR	Nestling DSR	Nest success (%)
Sprague's Pipit	13	11	65	0.944 ± 0.011	0.940 ± 0.013	24.0
Clay-colored Sparrow	11	9	84	0.925 ± 0.014	0.883 ± 0.018	13.9
Savannah Sparrow	11.5	9	84	0.952 ± 0.010	0.903 ± 0.015	22.7
Baird's Sparrow	11.5	9.5	182	0.949 ± 0.007	0.906 ± 0.011	21.7
Chestnut-collared Longspur	11.5	10	493	0.943 ± 0.004	0.918 ± 0.006	21.6
Western Meadowlark	13	11	104	0.943 ± 0.010	0.923 ± 0.012	19.2

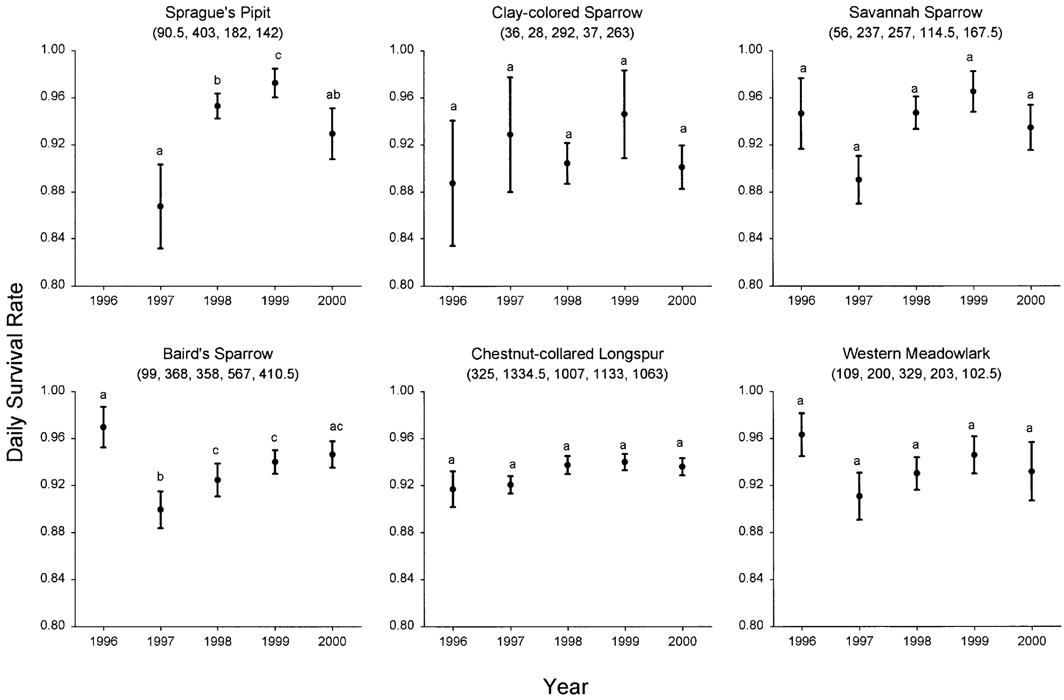

FIG. 3. Annual variation of mean (± SE) daily survival rates (incubation and nestling period combined) for six grassland songbirds in southern Saskatchewan, 1996–2000. Exposure days are in parentheses for each year. Years sharing the same letter do not differ significantly ($P > 0.05$, one-way ANOVA) from each other. No Sprague's Pipit nests were found in 1996.

42%, respectively) than during other years (6–23%). Savannah Sparrow and Western Meadowlark nests were not parasitized during 1999 and 2000, respectively. It is unknown whether variations in parasitism frequencies were linked to cowbird density, as cowbird densities were not quantified in 1996 and 1997.

Overall, cowbirds parasitized 15–29% of host nests in this study (Table 4). Savannah Sparrow, Clay-colored Sparrow and Western Meadowlark incurred the highest frequency of parasitism. The infrequent parasitism recorded for Sprague's Pipit and Chestnut-collared Longspur nests in this study is consistent with that found in Manitoba (Davis and Sealy 2000) and Montana (S. L. Jones unpubl. data). Although egg ejection by cowbird hosts could account for the low parasitism frequencies I observed, there are no published data on egg rejection behavior in Sprague's Pipits. However, Davis et al. (2002) found that the low parasitism frequency reported for longspurs (see Hill and Gould 1997) was not due to egg rejection. Instead, the authors suggested that other antiparasite strategies (e.g., nest defense behavior) might be responsible for the infrequent parasitism of longspurs.

One grassland host that appears to incur relatively high frequencies of parasitism is the Western Meadowlark. Despite reports from other regions that Western Meadowlarks recognize and reject cowbird eggs experimentally added to their nest (Peer et al. 2000), meadowlarks frequently were parasitized in this study (Table 4). In addition, high parasitism rates also have been reported in Manitoba (43%; Davis and Sealy 2000), Montana (30%; S. L. Jones unpubl. data), and North Dakota (47%; Koford et al. 2000). Other studies suggest that parasitism frequencies of grassland hosts vary geographically in the Great Plains (Koford et al. 2000). Maher (1973), for example, reported no parasitism of 15 meadowlark nests in Saskatchewan, and only 7% of Western Meadowlark nests were parasitized in Kansas (Hill 1976) and North Dakota (T. Grant and E. Madden unpubl. data).

Multiple parasitism was observed frequent-

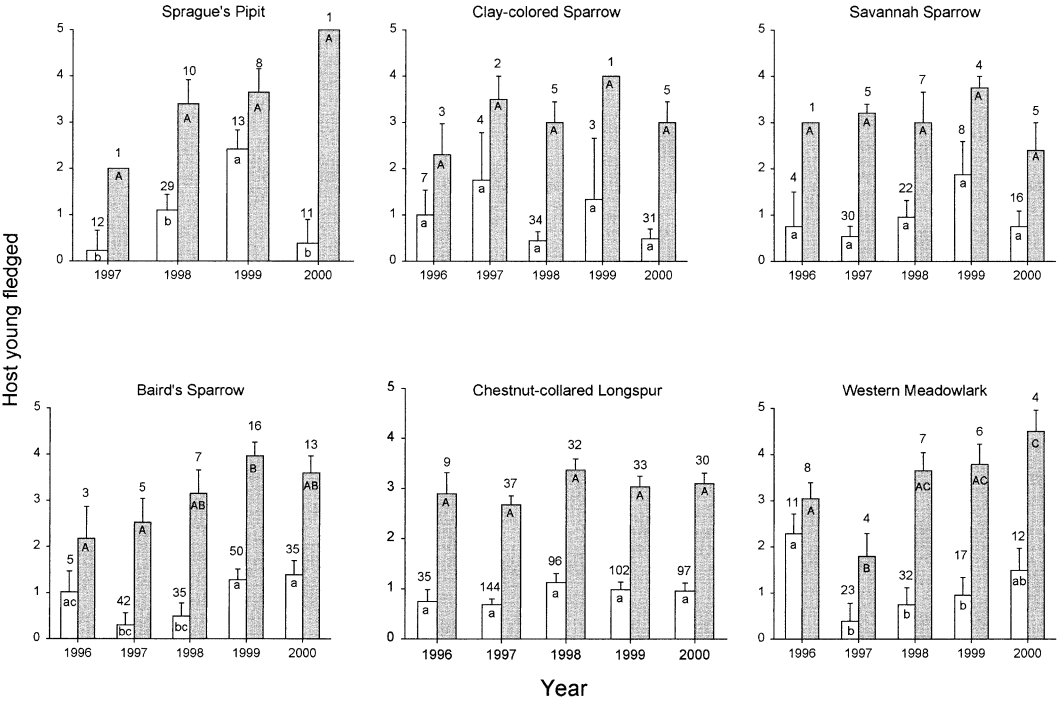

FIG. 4. Annual variation in mean (+SE) productivity for six grassland songbirds in southern Saskatchewan, 1996–2000. Sample sizes are above each bar for all nesting attempts (white bars) and successful nesting attempts (gray bars). Years sharing the same letter do not differ significantly ($P > 0.05$, one-way ANOVA) from each other.

ly in this study, as most parasitized nests contained as many as three cowbird eggs, except Clay-colored Sparrow and Western Meadowlark nests, which contained as many as two and four cowbird eggs, respectively. Western Meadowlark and Baird's Sparrow nests contained more cowbird eggs than any other grassland host in this study (Table 4). Davis and Sealy (2000) found that multiple parasitism was common in grassland hosts, as cowbirds laid 2.0–3.6 eggs per parasitized nest, and Western Meadowlarks received as many as eight cowbird eggs. Of the focal grassland birds in this study, Friedmann and Kiff (1985) listed only Savannah Sparrows, Clay-colored Sparrows, and Chestnut-collared Longspurs as hosts that are known to have reared cowbird young. However, both Western Meadowlarks

TABLE 4. Frequency and intensity of cowbird parasitism and cowbird productivity in nests of six common grassland hosts in southern Saskatchewan, 1996–2000. Sample sizes are in parentheses.

Species	Nests parasitized (%)	Parasitized nests with >1 cowbird egg (%)	Mean (± SE) number of cowbird eggs laid	Percentage of cowbirds fledged (cowbird eggs)	Mean (± SE) number of cowbirds fledged/nest	Mean (± SE) number of cowbirds fledged/ successful[a] nest
Sprague's Pipit	15.4 (65)	50.0 (10)	1.6 ± 0.22	0.0 (16)	0	0
Clay-colored Sparrow	26.8 (82)	27.3 (22)	1.3 ± 0.10	17.8 (22)	0.23 ± 0.11	1.00 ± 0.32 (5)
Savannah Sparrow	28.9 (83)	41.7 (24)	1.5 ± 0.15	11.1 (23)	0.17 ± 0.10	1.00 ± 0.00 (2)
Baird's Sparrow	20.9 (182)	60.5 (38)	1.7 ± 0.10	11.7 (36)	0.19 ± 0.09	0.70 ± 0.30 (10)
Chestnut-collared Longspur	16.3 (490)	27.5 (80)	1.3 ± 0.06	12.4 (76)	0.16 ± 0.05	0.40 ± 0.13 (20)
Western Meadowlark	25.2 (103)	61.5 (26)	1.8 ± 0.16	18.6 (24)	0.32 ± 0.13	0.70 ± 0.26 (10)

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

TABLE 5. Clutch size, hatching success and productivity ($\bar{x}$ ± SE) were lower in nests that were parasitized than in nests that were not. Sample sizes are in parentheses. Data are from southern Saskatchewan, 1997–2000.

Species	Clutch size		Host eggs hatched		Host eggs incubated full term that hatched		Host young fledged/nest		Host young fledged/successful nest[a]	
	Parasitized	Not	Parasitized	Not	Parasitized	Not	Parasitized	Not	Parasitized	Not
Sprague's Pipit	2.9 ± 0.60 (10)***	4.8 ± 0.12 (52)	0.2 ± 0.20 (9)***	2.7 ± 0.30 (53)	1.0 ± 1.00 (2)	3.2 ± 0.30 (45)	0.2 ± 0.20 (10)**	1.2 ± 0.25 (55)	2.0 ± 0.0 (1)	3.5 ± 0.32 (19)
Clay-colored Sparrow	2.4 ± 0.28 (20)***	3.8 ± 0.06 (57)	0.9 ± 0.26 (19)***	2.3 ± 0.23 (58)	1.4 ± 0.34 (12)*	2.6 ± 0.22 (51)	0.4 ± 0.19 (22)	0.6 ± 0.18 (56)	2.0 ± 0.32 (5)***	3.5 ± 0.22 (10)
Savannah Sparrow	2.9 ± 0.27 (21)***	4.4 ± 0.10 (53)	1.2 ± 0.31 (20)***	2.8 ± 0.26 (54)	1.8 ± 0.35 (14)***	3.3 ± 0.24 (44)	0.1 ± 0.09 (23)***	1.1 ± 0.22 (56)	1.0 ± 0.58 (3)**	3.2 ± 0.27 (19)
Baird's Sparrow	2.9 ± 0.19 (36)***	4.6 ± 0.05 (134)	1.5 ± 0.25 (34)***	2.7 ± 0.18 (128)	1.9 ± 0.26 (28)***	3.5 ± 0.17 (97)	0.6 ± 0.18 (37)	1.0 ± 0.15 (133)	2.1 ± 0.35 (10)***	3.9 ± 0.18 (34)
C-collared Longspur	3.2 ± 0.12 (78)***	4.2 ± 0.04 (381)	1.8 ± 0.17 (72)***	2.4 ± 0.10 (378)	2.3 ± 0.17 (54)***	3.2 ± 0.09 (287)	0.6 ± 0.13 (74)*	1.0 ± 0.08 (399)	1.9 ± 0.24 (24)***	3.2 ± 0.11 (119)
Western Meadowlark	4.0 ± 0.24 (25)***	5.1 ± 0.10 (66)	2.4 ± 0.38 (21)	2.6 ± 0.27 (73)	2.8 ± 0.36 (18)	3.4 ± 0.28 (56)	1.1 ± 0.31 (24)	1.0 ± 0.21 (71)	2.4 ± 0.41 (11)*	3.7 ± 0.26 (19)

[a] Nests fledging host or cowbird young.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

and Baird's Sparrows fledged cowbirds in this study (see also Davis and Sealy 1998, 2000). Sprague's Pipits failed to fledge cowbird young (Table 4), suggesting they are a poor quality host. Similarly, while Davis and Sealy (2000) found that pipits were capable of rearing cowbird young to fledging age in Manitoba, they recorded only one cowbird young fledging from nine eggs laid in pipit nests. Western Meadowlarks and Clay-colored Sparrows were especially productive hosts for cowbirds as they fledged the most cowbird young per parasitized nest.

Brown-headed Cowbirds typically lower the productivity of their hosts through egg removal or damage, and through competition with host nestlings (Payne 1977). Indeed, parasitized grassland hosts in this study experienced lower productivity due to a combination of reduced clutch size, hatching, and fledging success (Table 5). Davis and Sealy (2000) found that host egg removal was primarily responsible for the lower productivity in parasitized Baird's Sparrow nests in Manitoba. Although egg removal by cowbirds contributed to lower productivity of grassland hosts in the current study, as evidenced by the significantly smaller clutches in parasitized nests, all hosts also hatched fewer eggs in parasitized nests (Table 5). Cowbirds may have lowered hatching success of smaller hosts by incidentally damaging host eggs during the laying of their own eggs or when removing host eggs. Alternatively, cowbirds may have deliberately damaged or depredated host eggs during nest visits (Granfors et al. 2001). Overall, cowbirds cost grassland hosts between 1.3 and 2.2 young per successful nest (Table 5), similar to costs reported for hosts in Manitoba (Davis and Sealy 2000).

Conclusions.—The limited amount of demographic data on grassland birds in the northern Great Plains limits our ability to understand the life history of these species and to gain insight into causes of their population declines. Although nest predation was the most important factor associated with reproductive success of grassland songbirds in Saskatchewan, other factors, such as cowbird parasitism, may be equally or more important in other regions (Davis and Sealy 2000, Koford et al. 2000). Without additional information on aspects of their breeding ecology (e.g., propensity for renesting and raising multiple broods within a season) and other important demographic parameters (e.g., juvenile and adult survival), our understanding of the impact of nest predation and brood parasitism is incomplete. Also, this lack of information hinders our ability to identify population sources and sinks (Pulliam 1988) and to develop effective conservation measures for grassland birds. More studies are required to determine critical factors that influence the demography of grassland songbirds throughout the northern Great Plains.

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