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NESTING BIOLOGY OF DICKCISSELS AND HENSLOW'S SPARROWS IN SOUTHWESTERN MISSOURI PRAIRIE FRAGMENTS

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ABSTRACT.—According to data from the North American Breeding Bird Survey, populations of Dickcissel (*Spiza americana*) and Henslow's Sparrow (*Ammodramus henslowii*) have declined severely during the last 30 years. The reasons for their population declines seem to differ; habitat fragmentation on the breeding grounds has been suggested to have little negative impact on Dickcissels, but appears to be a major reason for Henslow's Sparrow declines. Previous reports on the status of Dickcissels and Henslow's Sparrows largely were based on density estimates without considering the nesting biology of the two species. My comparison of the nesting biology of Dickcissel and Henslow's Sparrow provides some insight into potential factors that might contribute to their population declines. During 1995–1997, I studied the nesting biology of Dickcissels and Henslow's Sparrows in fragments of native tallgrass prairie in southwestern Missouri. Both species had similar clutch sizes, rates of hatching success, and numbers of young fledged per successful nest. Dickcissels tended to have lower rates of nesting success and higher rates of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) than Henslow's Sparrows. Although several vegetation characteristics at the nest differed between successful and depredated nests in Dickcissels, no differences were found between successful and depredated Henslow's Sparrow nests or between parasitized and unparasitized Dickcissel nests. My results indicate that Dickcissels might reproduce less successfully than Henslow's Sparrows in southwestern Missouri, and might therefore be of higher conservation concern on the breeding ground than previously thought. *Received 27 January 1999, accepted 3 June 1999.*

Data from the North American Breeding Bird Survey indicated that populations of Dickcissel (*Spiza americana*) and Henslow's Sparrows (*Ammodramus henslowii*) have declined by about 39% and 91%, respectively, during the last 30 years (Peterjohn et al. 1994). The reasons for the declines are thought to differ between the two species: Dickcissels are assumed to have declined mainly because of poisoning on their South American wintering grounds (Basili and Temple 1995, Basili 1997), and are thought to be little affected by breeding habitat loss or fragmentation (Herkert et al. 1993). In contrast, the population decline of Henslow's Sparrows seems to be mainly caused by loss and fragmentation of suitable grassland habitat on their breeding grounds (Herkert 1994). However, status assessments of Dickcissels and Henslow's Sparrows are based largely on estimates of density or relative abundance, without considering the breeding ecology of the two species. A comparison of the breeding ecology of Dickcissels and Henslow's Sparrows might provide information on factors that could cause differential reproductive success in the two species. Such factors might include clutch sizes, rates of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*), rates of nest predation, and hatching and fledging rates. Vegetation characteristics at the nest site might differ between the species and cause one species to be more susceptible to nest predation or cowbird parasitism.

In southwestern Missouri, little information has been collected on the nesting success of passerines breeding in tallgrass prairie fragments. In this study I describe and compare nesting characteristics of the Dickcissel and the Henslow's Sparrow in fragments of native tallgrass prairie in southwestern Missouri between 1995 and 1997. Detailed analyses on the effect of fragment size, proximity to habitat edge, management practices, and landscape structure on density and nesting success of these species are described elsewhere (Winter 1998, Winter and Faaborg in press).

Dickcissel.—Dickcissels are grassland habitat generalists; they can be found breeding in a wide variety of grassland vegetation (Bent 1968). Because males often sing from elevated perches and females often place their nests above the ground, they tolerate a relatively

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large number of shrubs and trees. As with most polygynous species, the female generally tends both eggs and young alone.

In spite of their ability to use secondary habitats such as non-native grasslands or road right-of-way, Dickcissel populations have declined by about 39% since 1966 (Peterjohn et al. 1994). Population trends in Dickcissels are difficult to estimate because their abundance and distribution fluctuate considerably among years (Fretwell 1986), but habitat fragmentation did not seem to be responsible for their population declines (Herkert et al. 1993). Instead, poisoning of tens of thousands of birds on the wintering grounds has been suggested as cause for its population decline (Basili and Temple 1995, Basili 1997). Recent evidence indicates that habitat fragmentation on the breeding grounds might also have a negative impact on this species (Winter 1998, Winter and Faaborg in press).

Henslow's Sparrow.—Little is known about the nesting behavior of this inconspicuous species because of its furtive behavior and its tendency to spend most of its time on the ground (Bent 1968). Its highest densities occur in grasslands with tall, dense vegetation and a well-developed layer of litter (Wiens 1969, Robins 1971, Zimmerman 1988, Herkert 1994, Mazur 1996, Winter 1998). Based on the few existing nesting studies (Hyde 1939, Bent 1968, Robins 1971, Schulenberg et al. 1994, Rohrbaugh et al. in press), we know that this monogamous species generally nests close to the ground in tall dense vegetation, preferably within large clumps of litter.

With the destruction of tallgrass prairie and similar grassland habitats, the breeding range of Henslow's Sparrows has contracted considerably during the last 30 years, mainly in the northeastern, eastern, and northwestern parts of its range (Pruitt 1996). Although Henslow's Sparrows also nest in secondary habitats such as hayfields and reclaimed surface mines (see review in Swanson 1996), it has shown a consistent population decline (Peterjohn et al. 1994, Herkert 1997). Analysis of Christmas Bird Count data in the southeastern United States also indicates population declines on the wintering grounds (Butcher and Lowe 1990). The major reason for the large population decline of Henslow's Sparrows has been suggested to be loss and fragmentation of habitat on the breeding grounds (Herkert 1994). However, studies in Missouri, Kansas, and Ohio indicated that Henslow's Sparrows can occurr in even small fragments (see Winter 1998), and since 1988 its populations have been steadily increasing in Illinois (J. R. Herkert, pers. comm.).

STUDY SITES AND METHODS

Study area.—Between 1995 and 1997, I studied the nesting biology of Dickcissels and Henslow's Sparrows in 13 fragments of native tallgrass prairie in southwestern Missouri (approx. 37° 30′ N, 93° 30′ W; Winter 1998). Dominant grasses in the study area included big bluestem (*Andropogon gerardii*), little bluestem (*Schizochyrium scoparium*), and Indian grass (*Sorghastrum nutans*). Dominant forbs included sunflower (*Helianthus* spp.), milkweed (*Asclepias* spp.), blazing star (*Liatris spicata*), and sensitive briar (*Schrankia nuttallii*). Prairies were owned by the Missouri Department of Conservation, the Missouri Prairie Foundation, The Nature Conservancy, and the Missouri Department of Natural Resources and were actively managed by prescribed burning and haying (see Winter 1998).

Nest searching and monitoring.—Throughout each field season (early May to end of July) my field assistants and I located and monitored nests of all grassland species that we found, but focused our nest searching efforts on finding nests of Henslow's Sparrows and Dickcissels. Nests were found by walking across the study sites and adjacent areas of similar vegetation, while paying close attention to behavior and vocalizations of nearby adult birds. Most nests were found by observing adults (Dickcissels: 80%; Henslow's Sparrows: 56%). Behavioral patterns of adults that we used as clues that nests might be nearby were chipping, flying short distances away or around the observer, flushing close to the observer followed by a short flight, and carrying nest material, fecal sacs, or food. The location of a potential nest site was marked with a short length of flagging tape at three locations within 1 m of a potential nest site forming a triangle. We then retreated 10–30 m and tried to locate the nest when the bird returned. Nests also were located by flushing birds while randomly walking across the prairie (Dickcissel: 10%; Henslow's Sparrow: 30%). The remaining 10% and 14% of all nests, respectively, were found fortuitously; flushing birds while doing other research activities such as vegetation measurements or censusing. Because rope-dragging and systematic search were ineffective methods for nest finding in 1995, I did not use those methods in the following years.

We did not search for or monitor nests when vegetation was wet (after rain or heavy dew immediately after sunrise) to minimize disturbance of vegetation surrounding nests. Each nest was marked with a flag 5 m to the north and a small ribbon was placed about 30 cm south of those nests that were hard to find. Every 3–4 days nest fate was checked by walking past the nest to avoid creating "dead ends" that might lead nest predators to the nest. During each nest check we recorded the number of host and cowbird eggs and young, presence or absence of adults, and the state of the nest if the nest was found empty. An empty nest was considered successful if one or more of the following cues were observed: feces in the nest, feather sheaths in the nest, nest rim flattened, adults carrying food or chipping, or fledgling close to nest.

Nest vegetation.—Nest vegetation was characterized within one week after activity at a nest had ceased. Vegetation was measured at five locations around the nest site: directly at the nest and 0.5 m from the nest in each cardinal direction. At each of the five points I measured vegetation cover (Daubenmire 1959), the number of woody stems within each Daubenmire frame, vegetation height, litter depth, and visual obstruction (Robel et al. 1970; for a more detailed description see Winter 1998). For each nest I calculated the mean for each of the five measuring points, and used the mean of those five data points for further analysis.

Estimates of nesting success.—When calculating rates of nesting success, I excluded nests for which it was not possible to determine if predation happened before or after a nest was abandoned. This was true for nests that had small clutch sizes (1–2 eggs) and were depredated the next time the nest was checked. Those nests, however, were included for estimating rates of cowbird parasitism. For each year I estimated species specific probabilities of daily nest survival (Mayfield 1975) separately for incubation and nestling stages, and for the total nesting period. The total probability of nest survival was defined as the probability that a nest successfully survived incubation and nestling periods and fledged at least one young of the parental species. In the two species that I investigated, incubation begins with the laying of the last egg (Bent 1968). I used the following exponents to estimate the probability of nesting success over the entire nesting period; Dickcissel: 21 days (12 incubation days plus 9 nestling days), and Henslow's Sparrow: 20 days (11 incubation days plus 9 nestling days; Ehrlich et al. 1988). Standard errors for daily nest survival rates were calculated by using the formula for binomial distributions (Zar 1996). I used means and confidence intervals (Johnson 1979) to compare rates of nesting success among years and between incubation and nestling stages in each year. To allow comparison with other studies that did not use Mayfield estimates, I also present the apparent proportion of successful nests.

Statistical analyses.—Logistic regression was used to investigate if nesting success was related to the date in the breeding season. I calculated mean clutch size for each week in the breeding season and used linear regression analysis to investigate if clutch size varied during the nesting season. Because the number of nests found varied among weeks, I weighted the mean weekly clutch size by its standard error. For this analysis I used all unparasitized nests of the three years of the study.

Vegetation characteristics of depredated and successful Dickcissel and Henslow's Sparrow nests were compared with a two-tailed t-test. P-values were compared to the P-values obtained from a sequential Bonferroni adjustment (Rice 1989). The same analysis was used to compare characteristics between Dickcissel and Henslow's Sparrow nests. Dickcissel was the only species with enough parasitized nests to allow for statistical analysis. For this species, host clutch size, number of host fledglings, and nest characteristics of parasitized and unparasitized nests were compared with t-tests. Nesting success of unparasitized and parasitized Dickcissel nests were compared by using means and confidence intervals (Johnson 1979). Logistic regression was used to investigate if cowbird parasitism was related to the date in the breeding season. All data were analyzed with SAS (SAS 6.03 for PC; SAS Institute, Inc. 1988) and are presented as means and standard errors; the level of significance was set at 0.05.

RESULTS

Nesting biology.—Henslow's Sparrows typically arrived in the study area in early May, about 1–2 weeks earlier than most Dickcissels, and stopped nesting by the end of July, also about 1–2 weeks earlier than most Dickcissels (Fig. 1). The latest observed initiation of incubation in Henslow's Sparrows was 16 July. In contrast to Henslow's Sparrows, some Dickcissels were observed carrying nesting material in early August. Although most Dickcissels seem to have completed their nesting activity by the end of July, some might nest until the end of August. The peak of Dickcissel nest initiation did not occur until early June, and they continued to nest throughout June and early July (Fig. 1A). In contrast to Dickcissels, Henslow's Sparrows had two peaks of nest initiation, one in the second and third week of May, and one in the middle of June (Fig. 1B).

Dickcissels and Henslow's Sparrows had almost identical clutch sizes, hatching and fledging rates, and lengths of nestling stages (Table 1). Clutch size of Dickcissels and Henslow's Sparrows tended to decline with date in the breeding season but not significantly (Dickcissel: $F = 4.8$, $r^2 = 0.35$, df = 9,10, $P = 0.06$, slope = -0.05 ± 0.02; Henslow's Sparrow: $F = 5.0$, $r^2 = 0.38$, df = 8,9, $P = 0.06$, slope = -0.05 ± 0.02).

Nesting success.—The main cause of nest failure was nest predation; 86% of all failed Henslow's Sparrow nests and 84% of all failed Dickcissel nests were depredated (Table

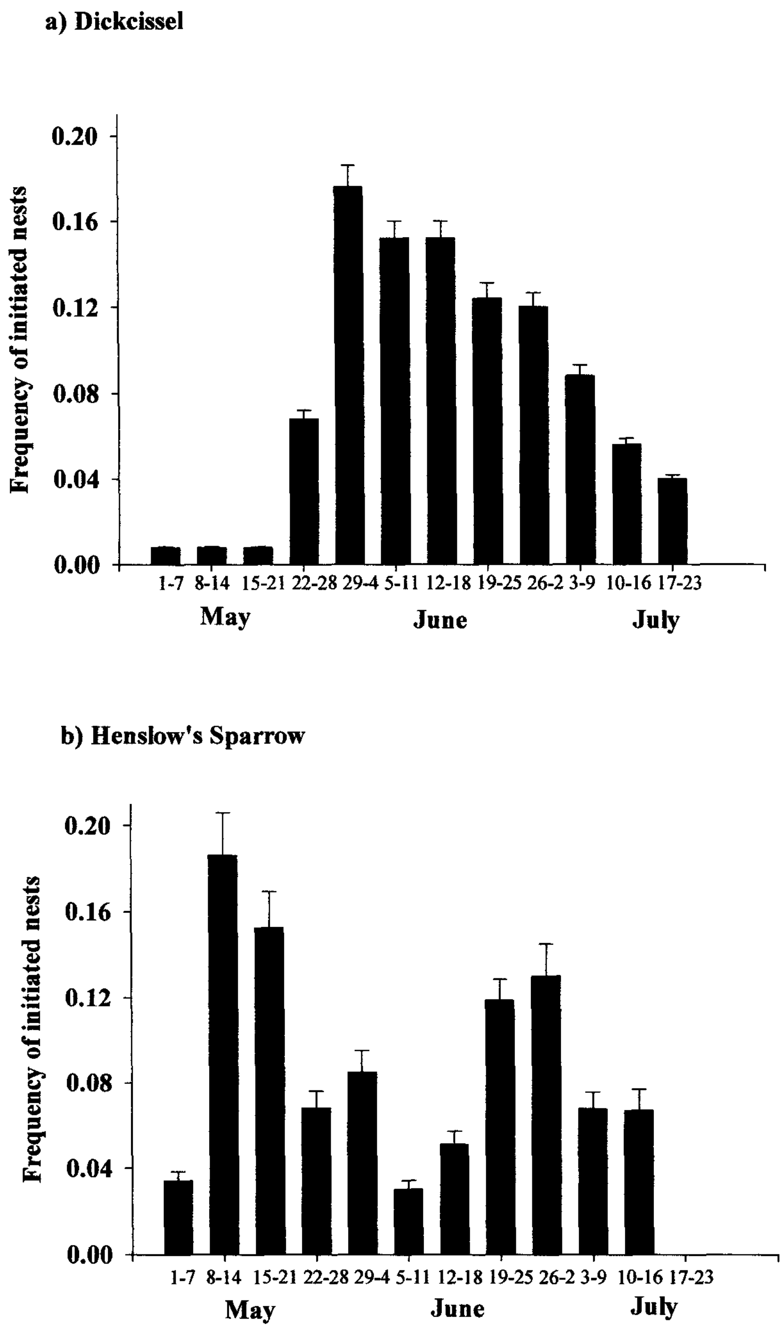

FIG. 1. Frequency distribution of clutch initiation dates in (A) Dickcissels and (B) Henslow's Sparrows in southwestern Missouri, 1995–1997.

1). Nest failure from unknown causes (probably weather) or nest abandonment were minimal (Table 1). None of the nests of either species failed as a result of cowbird parasitism. Dickcissel nesting success was lower during incubation than during the nestling stage in 1996, whereas nesting success during incubation and nestling stages did not differ

TABLE 1. General nesting data ($\bar{x} \pm$ SE) of Dickcissel and Henslow's Sparrow in southwestern Missouri prairie fragments, 1995–1997.

	Dickcissel (n = 242)[a]	Henslow's Sparrow (n = 59)
General nesting data:		
Successful nests (n)	112	34
Depredated nests (n)	128	25
Unknown loss (n)	2	0
Abandoned nests (n)[b]		
a) during nest building	13	0
b) with eggs	2	1
c) parasitized	3	0
Mowed nests (n)[c]	4	3
Nesting success:		
Mayfield nesting success (%)[d]	29.7	39.5
Apparent nesting success[e]	46.3	57.6
Nesting biology:		
Clutch size (n)[f]	3.9 ± 0.05 (227)	3.8 ± 0.10 (56)
Incubation days (n)[g]	11.45 ± 0.08 (11)	12.0 ± 0 (1)
Nestling days (n)[h]	8.7 ± 0.02 (52)	9.1 ± 0.08 (9)
Hatching success (n)[i]	92.9 (69)	93.2 (12)
Young fledged/nest	1.7	2.0
Young fledged/successful nest	3.6	3.5
Broad parasitism:		
Parasitized nests (%)[j]	8.8 ± 0.005 (21)	5.3 ± 0.006 (3)
Young fledged from successful unparasitized nests	3.7 ± 0.13 (105)	3.6 ± 0.25 (33)
Young fledged from successful parasitized nests	2.3 ± 0.26 (6)	2.0 ± 0 (1)

[a] Total number of nests found excluding those that were abandoned and mowed.
[b] Not included in the total number of nests.
[c] Not included in the total number of nests.
[d] After Mayfield (1975).
[e] Percent of successful nests from all nests found.
[f] Only unparasitized nests were used.
[g] n = number of nests that could be followed from nest building until hatching.
[h] n = number of nests that could be followed from hatching until fledging.
[i] Percent hatched eggs from all eggs for which the clutch size was known with certainty (see Methods).
[j] Percent of parasitized nests out of all nests found.

significantly in any other year or for Henslow's Sparrows (Table 2). Nesting success did not vary significantly with the date in the breeding season for either Dickcissels (Wald-χ^2 = 0.22, $P > 0.05$, n = 240) or Henslow's Sparrows (Wald-χ^2 = 2.66, $P > 0.05$, n = 59). Dickcissel nesting success was higher in 1997 than in 1996, whereas nesting success of Henslow's Sparrows did not vary significantly among years (Table 2). Mayfield nesting success tended to be higher in Henslow's Sparrows (40%) than in Dickcissels (30%; Tables 1, 2); however, the 95% confidence intervals for the estimates of nesting success in these two species overlapped.

Cowbird parasitism.—The rate of brood parasitism by Brown-headed Cowbirds was low, but slightly higher in Dickcissels (9.6%) than in Henslow's Sparrows (5.3%; Table 1). Dickcissel nests were parasitized throughout the nesting season except for the first and third week of May and the last week of July (Fig. 2).

Parasitized nests generally had smaller clutches, fewer fledglings, and lower nesting success than unparasitized nests (Table 3). On average, cowbirds laid 1.4 eggs per parasitized Dickcissel nest. None of the three parasitized Henslow's Sparrow nests had more than one cowbird egg. Host clutch size in both species was reduced by about 0.9 eggs per parasitized nest (Table 3). The reduction in clutch size was significant in Dickcissels (t = 4.07, df = 23, $P < 0.001$), with fewer host

TABLE 2. Nesting success of Dickcissel and Henslow's Sparrow in southwestern Missouri prairie fragments, 1995–1997.

Year	Nest cycle interval	n[a]	Depredated (n)[b]	Exposure days[c]	Survival ± SE[d]	Success (%)[e]
Dickcissel						
1995	Incubation	9	4	69.0	0.94 ± 0.03	21.6 < 48.8 < 100
	Nestling	12	4	74.5	0.95 ± 0.03	35.0 < 60.8 < 100
	Total[f]	18	8	143.5	0.94 ± 0.02	10.9 < 30.0 < 65.0
1996	Incubation	82	44	511.5	0.91 ± 0.01	24.7 < 34.0 < 44.5[g]
	Nestling	61	19	388.5	0.95 ± 0.01	52.0 < 63.7 < 76.0[g]
	Total	113	67	900.0	0.92 ± 0.01	12.0 < 19.7 < 24.9[g]
1997	Incubation	90	32	517.0	0.94 ± 0.01	36.8 < 46.4 < 61.3
	Nestling	98	30	618.0	0.95 ± 0.01	53.0 < 63.9 < 74.6
	Total	117	53	1235.0	0.96 ± 0.01	32.6 < 39.8 < 55.1[g]
All[h]	Incubation	181	80	1097.5	0.93 ± 0.01	34.0 < 40.3 < 51.4
	Nestling	171	53	1081.0	0.95 ± 0.01	46.4 < 63.6 < 70.6
	Total	248	128	2278.5	0.94 ± 0.00	21.8 < 29.7 < 34.0
Henslow's Sparrow						
1995	Incubation	6	0	34.5	1.0 ± 0.00	100.0
	Nestling	7	2	59.0	0.97 ± 0.02	52.0 < 73.3 < 100
	Total	7	2	83.5	0.98 ± 0.02	29.0 < 66.8 < 100
1996	Incubation	11	5	103.5	0.95 ± 0.02	35.4 < 58.0 < 89.5
	Nestling	16	8	146.0	0.94 ± 0.02	38.7 < 60.2 < 83.4
	Total	21	13	249.5	0.95 ± 0.01	23.4 < 34.3 < 54.4
1997	Incubation	14	4	84.5	0.95 ± 0.02	35.4 < 58.7 < 89.5
	Nestling	26	6	133.0	0.95 ± 0.02	42.8 < 66.0 < 91.0
	Total	31	10	217.5	0.95 ± 0.01	23.4 < 39.0 < 54.0
All	Incubation	31	9	222.5	0.96 ± 0.01	50.6 < 63.5 < 80.1
	Nestling	49	16	334.0	0.95 ± 0.01	52.0 < 64.3 < 76.0
	Total	59	25	550.5	0.95 ± 0.01	24.4 < 39.5 < 52.2

[a] Total number of nests monitored in a specific nesting interval during incubation and nestling stages. Because nests were mostly monitored during parts of both nesting stages, the sum of nests in each interval is higher than the total number of nests found.
[b] Total number of depredated nests.
[c] Total number of exposure days (Mayfield 1975).
[d] Probability of daily Mayfield nesting success (Day) = − (# depredated nests/# Mayfield days) + 1 SE = sqrt ((Day * (# depredated nests/# Mayfield days))/# Mayfield days).
[e] Probability of nesting success over the entire interval = Day$^{\text{interval length}}$, shown are means and lower and upper 95% confidence intervals (Johnson 1979).
[f] Both nesting stages combined.
[g] Intervals with the same letter do not overlap.
[h] All years combined.

young fledged from successful parasitized nests (t = 4.10, df = 34, P < 0.001). The reduction in nesting success was not caused by competition with cowbird young, but rather by a higher predation rate on parasitized nests; all successful parasitized nests fledged young of both host and cowbird.

Nest characteristics.—Compared to Henslow's Sparrows, Dickcissels chose a variety of nest sites. Most (45%) nests were placed in forbs, especially leadplant (*Amorpha canescens*) and ashy sunflower (*Helianthus mollis*), but shrubs (29%), grass (16%), and litter (10%) also were used as nesting substrates. Nests were typically woven in the stems of forbs or woody plants. Because nest searches were restricted to grassland habitat, nests were not found within shrubby edge habitats. However, many Dickcissels were observed breeding in such edge habitats (Winter 1998). Successful nests had taller vegetation, greater visual obstruction values, greater coverage by grass, and smaller areas of bare soil than unsuccessful nests (Table 4). None of the vegetative characteristics that I measured at Dickcissel nest sites differed between parasitized and unparasitized nests (Table 4).

Henslow's Sparrows typically placed their nests among layers of thick litter (82% of all nests). Compared to Dickcissel nests, the vegetation surrounding Henslow's Sparrow nests had deeper litter (3.5 ± 0.27 vs 1.9 ± 0.23

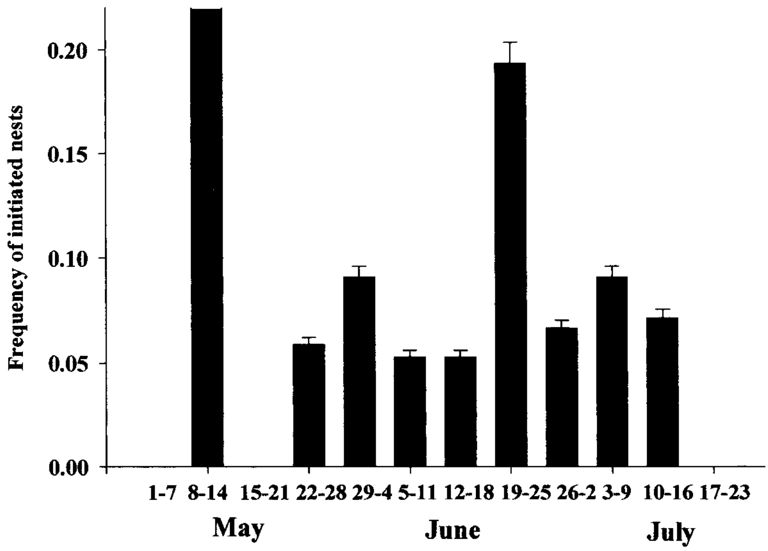

FIG. 2. Frequency distribution of rates of cowbird parasitism on Dickcissel nests in southwestern Missouri, 1995–1997.

cm; t = 3.3, df = 296, P = 0.001), lower vegetation (42.0 ± 1.12 vs 46.1 ± 0.67 cm; t = −2.8, df = 296, P = 0.005), greater cover by litter (29.6 ± 2.0 vs 11.6 ± 0.71%; t = 10.4, df = 296, $P < 0.001$), and less cover by forbs (17.9 ± 1.03 vs 26.0 ± 0.83%; t = −4.6, df = 296, $P < 0.001$), woody plants (1.5 ± 0.12 vs 5.2 ± 0.62%; t = −2.9, df = 296, P = 0.004), and soil (0.4 ± 0.12 vs 4.8 ± 0.40%; t = −5.5, df = 296, $P < 0.001$). Henslow's Sparrow nests also had a higher percentage of nest cover (90.3 ± 2.68 vs 67.7 ± 1.79%; t = 5.9, df = 296, $P < 0.001$), and were located closer to the ground (7.2 ± 0.53 vs 18.4 ± 1.04 cm; t = −5.4, df = 134, $P <$ 0.001). All significant P-values remained significant after a sequential Bonferroni adjustment. Henslow's Sparrows were never observed to place their nest within or in immediate proximity to woody vegetation. In contrast to Dickcissels, Henslow's Sparrows did not weave their nests into the surrounding vegetation, but placed them loosely among the surrounding stems of grass and dead vegeta-

TABLE 3. Clutch size ($\bar{x}$ ± SE) and nesting success of unparasitized and parasitized nests in Dickcissel and Henslow's Sparrow in southwestern Missouri, 1995–1997.

	Unparasitized nests					Parasitized nests					
Year	n	Clutch size	Exposure days	Failed nests	Success[a] (%)	n	Host clutch	Cowbird clutch	Exposure days	Failed nests	Success (%)
Dickcissel											
1995	17	3.9 ± 0.13	143.5	7	35.0	1	3.0 ± 0	2.0 ± 0	12.0	1	16.1
1996	104	3.9 ± 0.07	931.0	62	23.5	5	3.4 ± 0.40	2.0 ± 0.55	26.0	5	1.1
1997	98	3.9 ± 0.07	1014.5	44	39.4	15	3.0 ± 0.26	1.2 ± 0.14	152.0	9	27.7
All	220	3.9 ± 0.05	2089.0	113	31.2	21	3.0 ± 0.22	1.4 ± 0.18	190.0	15	17.8
Henslow's Sparrow											
1995	6	4.3 ± 0.21	79.0	2	59.9	1	3.0 ± 0	1.0 ± 0	15.0	0	100
1996	21	3.7 ± 0.17	138.0	13	13.8	0	N/A	0	N/A	N/A	N/A
1997	29	3.7 ± 0.15	201.5	8	44.5	2	3.0 ± 0	1.0 ± 0	16.5	2	7.5
All	56	3.8 ± 0.10	418.5	23	32.3	3	3.0 ± 0	1.0 ± 0	31.5	2	26.9

[a] Probability that a nest survived both incubation and nesting periods, estimated after Mayfield (1975).

TABLE 4. Dickcissel nest characteristics ($\bar{x} \pm$ SE) in successful and depredated nests, and non-parasitized and parasitized nests in southwestern Missouri prairie fragments, 1995–1997. All significant *P*-values remained significant after a Bonferroni adjustment.

	Nest success					Nest parasitism				
Variable	Successful (n = 106)	Depredated (n = 109)	t	df	P	Unparasitized (n = 197)	Parasitized (n = 18)	t	df	P
Litter depth (cm)	2.0 ± 0.22	1.5 ± 0.19	−1.6	213	0.11	1.8 ± 0.15	1.4 ± 0.41	0.8	213	0.40
Vegetation height (cm)	48.9 ± 0.85	44.4 ± 1.03	−3.4[a]	209	<0.001	46.8 ± 0.72	43.9 ± 2.16	1.1	213	0.25
Visual obstruction (dm)	29.6 ± 0.80	25.9 ± 1.13	−2.7[a]	195	<0.008	27.8 ± 0.69	26.6 ± 4.02	0.3[a]	18	0.77
No. woody stems	0.4 ± 0.08	0.6 ± 0.11	1.3[a]	203	0.18	0.5 ± 0.07	0.7 ± 0.24	−0.8	215	0.44
Litter cover (%)	11.2 ± 0.92	11.4 ± 0.99	0.2	215	0.84	11.4 ± 0.72	10.2 ± 1.91	0.5	215	0.60
Grass cover (%)	56.0 ± 1.26	50.7 ± 1.09	−3.2	215	0.002	53.6 ± 0.89	48.8 ± 2.47	1.6	215	0.11
Forb cover (%)	25.9 ± 1.36	27.1 ± 1.10	0.7	215	0.49	26.2 ± 0.89	29.2 ± 3.49	−1.0	215	0.33
Woody cover (%)	4.2 ± 0.78	5.1 ± 0.96	0.7[a]	210	0.51	4.4 ± 0.63	7.4 ± 2.95	−1.0[a]	19.7	0.19
Soil cover (%)	3.6 ± 0.45	5.7 ± 0.66	2.6[a]	194	0.009	4.7 ± 0.44	4.4 ± 1.25	0.2	215	0.85
Nest cover (%)	69.2 ± 2.79	64.8 ± 2.54	−1.2	217	0.23	66.2 ± 1.97	73.5 ± 6.34	−1.1	217	0.26
Nest height (cm)	18.7 ± 1.49	17.6 ± 1.49	−0.5	98	0.61	18.3 ± 1.15	17.6 ± 2.69	0.2	98	0.83

[a] t- and P-values for non-equal variance.

tion. In late June and throughout July, 18% of all nests were found in areas that had been burned the same spring and therefore lacked any litter. In these areas, Henslow's Sparrows placed their nests within large clumps of grass (mostly big bluestem and Indian grass) close to the ground. Successful and depredated Henslow's Sparrow nests did not differ in any nest characteristic (Table 5).

DISCUSSION

In southwestern Missouri, Dickcissels and Henslow's Sparrows had nearly identical clutch size, hatching success, length of incubation and nestling stages, and number of young fledged per successful nest. These variables were similar to previous reports for Dickcissels (Bent 1968, Harmeson 1974, Zimmerman 1982, Fretwell 1986, Patterson and Best 1996). Fewer studies have monitored Henslow's Sparrow nests, because their nests are difficult to locate (Bent 1968; Robins 1971; Schulenberg et al. 1994; D. Reinking, pers. comm.). Clutch size of Dickcissels and Henslow's Sparrows tended to decrease with date in the breeding season in southwestern Missouri. For Dickcissels, Harmeson (1974) described a peak in clutch size in the middle of the nesting season, whereas changes of Henslow's Sparrow clutch size over time had not yet been described.

Although Dickcissels and Henslow's Sparrows had almost identical nesting variables, their nesting phenologies seemed to differ. Generally, nesting success is relatively low in most grassland nesting birds, varying from 25–50% (Wiens 1969, Vickery et al. 1992, Martin 1995). Grassland birds often compensate for low nesting success by several renesting attempts throughout the breeding season. Consequently, most grassland nesting species raise an average of 1.5–2 broods per female per year (Wiens 1969, Martin 1995). The single nesting peak of Dickcissels in my study seemed to indicate that Dickcissels raised only one brood in my study area, as has been described by Zimmerman (1982, 1984). However, E. Bollinger (pers. comm.) observed a second brood in one color-banded Dickcissel female, indicating that Dickcissels can be double-brooded. Because Dickcissels appear to frequently move within one breeding season (Fretwell 1986), possibly because of displace-

TABLE 5. Henslow's Sparrow nest characteristics ($\bar{x} \pm$ SE) at successful and depredated nests in southwestern Missouri prairie fragments, 1995–1997.

Variable	Successful (n = 35)	Depredated (n = 25)	t	df	P
Litter depth (cm)	3.3 ± 0.37	3.7 ± 0.41	0.72	58	0.47
Vegetation height (cm)	43.0 ± 1.48	40.7 ± 1.71	−1.00	58	0.32
Visual obstruction (dm)	25.4 ± 1.89	24.9 ± 2.09	−0.20	57.7	0.84
No. woody stems	0.43 ± 0.14	0.26 ± 0.11	−0.94	57.7	0.35
Litter cover (%)	27.1 ± 2.70	33.1 ± 2.85	1.50	58	0.14
Grass cover (%)	51.4 ± 2.50	49.4 ± 2.43	−0.57	58	0.57
Forb cover (%)	19.1 ± 1.35	16.2 ± 1.58	−1.42	58	0.16
Woody cover (%)	1.82 ± 0.68	1.14 ± 0.45	−0.98	55.2	0.40
Soil cover (%)	0.55 ± 0.12	0.22 ± 0.11	−1.47	50.4	0.15
Nest cover (%)	89.6 ± 4.02	91.7 ± 3.03	0.41	57.7	0.68
Nest height (cm)	7.0 ± 0.63	7.9 ± 1.02	0.74	26.8	0.47

ment from hayfields after mowing (Igl 1991, Frawley and Best 1991), females might renest or raise a second brood in another area. None of the Dickcissels in my study area were color-banded; therefore, I could not determine if late nesting females (as also described by Harmeson 1974) had arrived from other areas, or if they had started a second brood or a renesting attempt in the same area.

Henslow's Sparrows seemed to be more likely to be double-brooded in southwestern Missouri than Dickcissels because they clearly exhibited two peaks of nest initiation. However, as with Dickcissels, individual birds were not color-banded, making it impossible to determine if the second nesting peak was caused by females on their second brood, by renesting attempts, by newly arriving females, or if it was an artifact of small sample size. This lack of adequate information is also true for all other studies that describe this species as double-brooded (Hyde 1939, Bent 1968, Robins 1971).

Nest predation was the main reason for nest failure, as has been described for many other bird species (Martin 1993, Patterson and Best 1996). Mean Mayfield nesting success of Dickcissels was similar to that reported from Kansas (Zimmerman 1984) and Missouri Crop Reserve Program fields (McCoy 1996), but lower rates of nesting success were reported from Iowa (Bryan and Best 1994, Patterson and Best 1996), Kansas (Hill 1976), and Oklahoma (Rohrbaugh et al. in press). Robins (1971) reported that 6 of 11 Henslow's Sparrow nests found in Michigan successfully fledged young. This apparent success rate (54.5%) is comparable to the apparent success rate in my study (57.6%). However, the number of young fledged per nest in Michigan (0.37) and the number of young fledged per successful nest (2.8) were lower than in Missouri. In Oklahoma, 40.9% of 22 Henslow's Sparrow nests were successful (D. Reinking, pers. comm.), which was about 17% lower than in Missouri. The number of young fledged per unparasitized Henslow's Sparrow nest was also slightly lower in Oklahoma than in Missouri (3.3 vs 3.6 young fledged per nest; Reinking, pers. comm.). Southwestern Missouri thus seems to be a relatively productive breeding area for Henslow's Sparrows.

Daily Mayfield nesting success in Dickcissels was lower during incubation than during nestling stages in 1996, and tended to be lower in 1995 and 1997. Higher nesting success during the nestling stage was also reported by Bryan and Best (1994) and by Harmeson (1974), and generally is the most frequently observed pattern of nest survival (Nice 1957; but see Patterson and Best 1996). Nesting success could be lower during incubation because poorly concealed nests are the first to be found by nest predators, or because visually hunting nest predators find nests with eggs more easily. Shorter and sparser vegetation at depredated Dickcissel nests indicated that these nests were in fact less well concealed than successful nests. High incidence of nest predation by mammals (see Winter 1998), which hunt based on visual and olfactory cues, might explain the tendency for slightly lower nesting success during incubation in southwestern Missouri. However, the only nest predators that I observed at Dickcissel nests were two snakes, one eastern yellowbellied racer (*Coluber constrictor flaviventris*) and one prairie kingsnake (*Lampropeltis calligaster calligaster*). Because rates of nesting success in Henslow's Sparrows were nearly identical during incubation and nestling stages, and because their nests were extremely well concealed, it seems that visually hunting nest predators rarely destroy its nests. Instead of visually hunting predators, snakes are possibly the main nest predators of Henslow's Sparrow nests. This could also be the reason why nest vegetation did not differ between successful and depredated nests.

Rates of brood parasitism by Brown-headed Cowbirds in southwestern Missouri were relatively low compared to parasitism rates described in other studies on grassland-nesting birds (Hergenrader 1962; Zimmerman 1966, 1983; Hill 1976; Elliott 1978; Patterson and Best 1996; Koford et al. in press). Because cowbirds did not cause direct mortality to any Dickcissel young in my study, brood parasitism by itself did not directly decrease nesting success. However, the reduction in clutch size decreased the number of host fledglings by about one young per parasitized nest, as also was reported by Hill (1976).

In Henslow's Sparrows, brood parasitism by Brown-headed Cowbirds was slightly lower than in Dickcissels; only 5% of all Henslow's Sparrow nests were parasitized in southwestern Missouri. The only other records of parasitized Henslow's Sparrow nests are from Oklahoma (Reinking, pers. comm.) and Kansas (Schulenberg et al. 1994). In Oklahoma, 2 out of 22 Henslow's Sparrow nests were parasitized. Only 1 of the parasitized nests successfully fledged both host and cowbird young, whereas the other nest was depredated. The one Henslow's Sparrow nest that was found by Schulenberg and coauthors (1994) in Kansas contained two cowbird eggs and was abandoned during incubation. Cowbird parasitism is probably low in Henslow's Sparrows because their nests are well concealed. Low parasitism rates in Henslow's Sparrows were previously noted by Bent (1968:786), who mentioned that this species "appears to escape heavy parasitism, possibly because the nests are so well hidden."

Nest placement differed significantly between Dickcissels and Henslow's Sparrows. Dickcissels chose a variety of nesting habitats (Bent 1968); they preferred forbs and shrubs, and did not avoid edge habitats. Henslow's Sparrow nests, on the other hand, were never found in either of the nest substrates preferred by Dickcissels or within shrubby edge habitat. Instead, this species built its nest lower to the ground, mainly within large clumps of litter where it was almost 100% covered by vegetation (Hyde 1939, Robin 1971, Schulenberg et al. 1994). Several researchers that described the relationship between Henslow's Sparrow breeding densities and vegetation parameters also noted the species' preference for tall grass and litter cover (Wiens 1969, Skinner et al. 1984, Herkert 1994, Swanson 1996). I found that Henslow's Sparrows were able to build nests in recently burned areas that lacked litter, as did Zimmerman (pers. comm. in Schulenberg et al. 1994) in Kansas. Because Dickcissel nests were more conspicuous than Henslow's Sparrow nests, they were probably more easily detected by visually hunting nest predators and Brown-headed Cowbirds, resulting in slightly higher rates of nest predation and nest parasitism in this species.

General nesting data indicated that Dickcissels tended to be less productive in southwestern Missouri than Henslow's Sparrows. These findings are in contrast to the general notion that Dickcissels are of little conservation concern on the breeding grounds (Herkert et al. 1993, Swanson 1996). The discrepancy may be because previous reports on Dickcissels and Henslow's Sparrows were based only on breeding density estimates. This study showed that basic data on the general nesting ecology of a species are necessary for a better understanding of the factors that might influence a species in a given area.

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