NEST-SITE SELECTION PATTERNS AND THE INFLUENCE OF VEGETATION ON NEST SURVIVAL OF MIXED-GRASS PRAIRIE PASSERINES

NEST-SITE SELECTION PATTERNS AND THE INFLUENCE OF VEGETATION ON NEST SURVIVAL OF MIXED-GRASS PRAIRIE PASSERINES

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Abstract. Identification of habitat features influencing reproduction and survival are essential for the management and long-term viability of grassland bird populations. I quantified vegetation structure at nests and random sites in southern Saskatchewan, Canada, to determine which microhabitat features are important in nest-site selection by Sprague's Pipit (*Anthus spragueii*), Savannah Sparrow (*Passerculus sandwichensis*), Baird's Sparrow (*Ammodramus bairdii*), Chestnut-collared Longspur (*Calcarius ornatus*), and Western Meadowlark (*Sturnella neglecta*). In addition, I related microhabitat features to nest survival to determine whether predation might influence their choice of nest sites. Grassland passerines exhibited nonrandom nest-placement patterns and built their nests in sites that were characterized by a greater density of dead vegetation within 30 cm of the ground, increased amounts of litter, and reduced coverage of bare ground. In addition, each species nested in taller vegetation than that found at random sites. However, nests were partitioned along a vegetation gradient ranging from relatively short and sparse (e.g., Chestnut-collared Longspur) to relatively tall and dense (e.g., Western Meadowlark). Nest survival varied with time-specific variables (nest age and date) and year, with nest-site vegetation explaining additional variation not accounted for by these effects. However, vegetation effects were highly variable compared to age effects. Diverse predator communities, spatial and temporal variation in selection pressures, and other constraints may account for inconsistent relationships between nest survival and nest-site characteristics for grassland passerines.

Key words: grassland songbirds, mixed-grass prairie, nest predation, nest-site selection, nest survival, vegetation structure.

Patrones de Selección de Sitios de Nidificación y la Influencia de la Vegetación en la Supervivencia de Nidos de Aves Paserinas de Praderas de Pastos Mixtos

Resumen. La identificación de las características del ambiente que influencian la reproducción y la supervivencia son esenciales para el manejo y la viabilidad al largo plazo de las poblaciones de las aves de pastizal. Cuantifiqué la estructura de la vegetación alrededor de los nidos y en sitios aleatorios en el sur de Saskatchewan, Canadá, para determinar cuáles rasgos micro-ambientales son importantes en la selección de nidos por parte de *Anthus spragueii*, *Passerculus sandwichensis*, *Ammodramus bairdii*, *Calcarius ornatus* y *Sturnella neglecta*. Adicionalmente, relacioné los rasgos micro-ambientales con la supervivencia de los nidos para determinar si la depredación podría influir sobre la elección de los sitios de nidificación. Las aves paserinas de pastizal mostraron patrones no aleatorios de ubicación de los nidos y construyeron sus nidos en sitios que se caracterizaron por una densidad más alta de vegetación muerta en los primeros 30 cm desde el suelo, una mayor cantidad de hojarasca y una baja cobertura de suelo desnudo. Adicionalmente, cada especie nidificó en sitios con vegetación más alta que la de los sitios elegidos al azar. Sin embargo, los nidos se distribuyeron a lo largo de un gradiente de vegetación desde relativamente corta y esparcida (e.g., *Calcarius ornatus*) a relativamente alta y densa (e.g., *Sturnella neglecta*). La supervivencia de los nidos varió en relación con variables que dependen del tiempo (edad del nido y fecha) y del año, mientras que la vegetación de los sitios donde se ubicaron los nidos explicó una parte adicional de la variación no explicada por estos factores. Sin embargo, los efectos de la vegetación fueron muy variables comparados de modo general con los efectos de la edad. Las diferencias en las comunidades de depredadores, la variación espacial y temporal en las presiones de selección y otras limitantes podrían explicar las

relaciones inconsistentes entre la supervivencia de los nidos y las características de los sitios de nidificación para las aves paserinas de pastizal.

INTRODUCTION

Conservation of remaining tracts of grassland habitat and the identification of habitat features influencing reproduction and survival are essential for the management and long-term viability of grassland bird populations. Most studies to date have quantified bird abundance or occurrence to identify habitat features selected by grassland birds (Johnson and Schwartz 1993, Herkert 1994, Madden et al. 2000). Although these types of studies have advanced our understanding about habitat requirements of grassland birds, their results could be misleading if abundance or occurrence is not a good indicator of habitat quality (Van Horne 1983, Vickery et al. 1992). Identifying habitat features important in nest-site selection offers the advantage of measuring habitat features at known breeding locations and the ability to correlate microhabitat variables with reproductive success. However, few studies have attempted to determine which habitat features are important in nest-site selection for grassland birds (With and Webb 1993, Sutter 1997), and fewer have linked reproductive success to nest-site features (Wray and Whitmore 1979, With 1994, Winter 1999).

Nest predation has been identified as the primary factor responsible for reproductive failure in grassland birds (Best et al. 1997, Koford 1999, Davis and Sealy 2000). Thus, natural selection should favor individuals that nest in sites that are less prone to predation if habitat choices are genetically based (Martin 1998). Such choices may occur at the scale of the nest-site itself and at larger spatial scales such as the habitat patch surrounding the nest site. For example, birds could reduce the likelihood of predation by nesting in sites that reduce visual, auditory, and olfactory cues to predators (Martin 1993) and nest in heterogeneous habitat patches comprising a number of suitable sites that subsequently reduce the searching efficiency of predators (Bowman and Harris 1980, Martin 1993). Birds may also reduce the likelihood of predation by selecting nests sites that differ from other locally sympatric species (Martin 1996).

I quantified vegetation characteristics at nest sites on native mixed-grass prairie pastures to identify microhabitat features important in nest-

site selection and determine whether vegetation structure influences nest survival of five grassland passerines (Sprague's Pipit [*Anthus spragueii*], Savannah Sparrow [*Passerculus sandwichensis*], Baird's Sparrow [*Ammodramus bairdii*], Chestnut-collared Longspur [*Calcarius ornatus*], and Western Meadowlark [*Sturnella neglecta*]). Specifically, my objectives were to determine 1) which microhabitat features are selected (based on use versus availability) by nesting prairie passerines, 2) how species differ in their choice of nest sites, and 3) whether microhabitat characteristics influence nest survival.

METHODS

STUDY AREA

My study was conducted as part of a larger study examining the effects of patch size on grassland passerine reproductive success (Davis 2003a). I conducted the study on native prairie pastures in the eastern portion of the Mixed and Moist-mixed Grassland ecoregions of southern Saskatchewan during 1997–2000 (49°45′N, 105° 45′W). The study area comprised 12 rural municipalities totalling approximately 10 500 km². I selected study sites from patches of native mixed-grass prairie identified from 1:20 000 aerial photographs in 1997 and 1998, and classified Landsat thematic mapper imagery in 1999 and 2000. I identified a pool of potential patches from three size categories (<65 ha, 65–256 ha and >256 ha) in each year of the study. A subset of patches was then randomly selected from each size category. I visited grassland patches identified from aerial photographs and satellite images prior to the field season to determine their suitability and retained pastures only if they had never been cultivated, were in fair-to-excellent range condition (Task Group on Unity in Concepts and Terminology 1995), and had experienced light-to-moderate grazing intensity the previous year. These criteria were chosen to reduce confounding effects of vegetation on pasture size, to increase the likelihood of use by high-priority species (i.e., Baird's Sparrow and Sprague's Pipit), and to ensure a similar bird community among sites. Ultimately, I was restricted to pastures where landowners permitted access to their land. Different pastures were se-

lected each year. Although this potentially confounds year and site effects, it allowed greater spatial replication of sites. A total of 41 pastures were included in the study, with nest vegetation quantified on 38 of the sites (see Davis 2003a for details).

NEST LOCATION AND MEASUREMENTS

I established a 16-ha study plot near the center of each pasture and partitioned it into 50-m grids with bamboo stakes (approx. 50 cm in length) and surveyor flags. Nest searching and monitoring were conducted in the study plots from early May to early August, 1997–2000. Nest searches were typically conducted between 07:30 and 14:00 (CST) by flushing adults from their nests using a weighted 25-m nylon rope with aluminium and tin cans attached every 0.5 m. Nests were also located fortuitously while conducting other activities on the pastures throughout the day. Nests were marked with surveyor flags and bamboo stakes 5 m away and inspected every 2–5 days until the young fledged or the nesting attempt ended. Nest attempts were considered successful if at least one host nestling fledged the nest. Cues such as adult(s) uttering alarm calls nearby, minimal nest disturbance, the presence of feces and feather scales in the nest, and nestling age were all used to determine nest fate.

I quantified vegetation structure of most nests (81%) within two weeks after the nesting attempt was completed. I excluded any nest that had not been measured within 21 days of its termination. I passed a metal rod vertically through the vegetation (Rotenberry and Wiens 1980) and recorded the number of contacts by different vegetation types (live grass, standing dead grasses, forbs, shrubs ≥15 cm, and dwarf shrubs <15 cm) in successive 10-cm height intervals. Grasses were categorized as live and dead because dead vegetation is the primary source of cover available at the beginning and throughout the breeding season whereas live grasses offer better nesting cover as the season progresses. Shrubs were divided into short and tall because many grassland species avoid areas with tall, dense shrubs (Madden et al. 2000), but will place their nests in association with short, sparse shrubs (pers. obs.). I dropped the rod near the outer edge of the nest rim at each of the four ordinal points and in the center of the nest. I measured vegetation height at the highest contact for each of the five locations (north, south east, west, and

center) and depth of litter (unconsolidated plant material no longer attached to the ground) was measured adjacent to the nest bowl at each of the ordinal points. Distance from the center of the nest to the nearest shrub was also recorded. I estimated the percent cover of bare ground and cattle dung within a 50 × 50 cm quadrat centered on the nest. These sampling procedures were repeated for eight random locations within 30 m of each nest in 1997–1998, and four random locations in 1999–2000. Random measurements were restricted to grassland habitat (e.g., no wetlands or riparian habitats) and also to within 30 m of the nest in an attempt to stay within each species' territory. Random measurements were taken in an area that approximated the circumference of the nest and were measured on the same day as nest sites. Means of random values were used for subsequent analyses. Nests of all species were measured in 1997–1999, but only Sprague's Pipit and Baird's Sparrow nests were quantified in 2000 due to logistical constraints.

I assessed nest visibility at nest sites using a thin plastic disk divided into eight black-and-white pie-shaped sections (Davis and Sealy 1998). I placed the disk inside the nest and recorded the number of visible sections from 1 m away at five points (each cardinal direction and directly overhead). Thus visible nests scored higher (maximum = 40 sections observed) than well-concealed nests (minimum = 0 sections observed).

STATISTICAL ANALYSIS

All analyses were conducted using SAS ver. 8 (SAS Institute, Inc. 1999). A total of 26 nest vegetation variables were quantified overall. Canonical descriminant analyses (PROC CANDISC) was used to identify linear combinations of nest vegetation variables that best identified structural differences among the species' nest sites. I also performed factor analysis (PROC FACTOR) using a principal components solution to reduce the 26 variables to a smaller set of uncorrelated factors for consideration in nest-site selection and nest survival models (see below). Factors with an eigenvalue >1 were retained and a varimax rotation method was used to facilitate interpretation of factor loadings. A total of 10 factors were identified that could be reasonably interpreted and that reflected struc-

tural gradients I considered important in nest-site selection by grassland passerines.

I used Akaike's Information Criterion score corrected for small sample sizes (AIC$_c$, Burnham and Anderson 1998) to identify nest-site selection and nest survival models best fitting the data. AIC$_c$ weights were calculated based on all candidate models according to Burnham and Anderson (1998) and represent the likelihood that a particular model is the best model given the data and the candidate models considered. I employed model averaging to quantify parameter estimates and unconditional standard errors if there was little support for a single best model (Burnham and Anderson 1998). Parameter estimates with 90% confidence excluding zero were considered to be influential.

Nest-site selection models. I used a multivariate matched pairs logistic regression analysis and a backward elimination procedure to fit candidate models by sequentially removing variables with the largest *P*-value based on likelihood-ratio tests. This regression analysis was used because each nest was paired with its own unique random points (Stokes et al. 2000, Liebezeit and George 2002). All nests were included in the analysis, regardless of nest fate. The model with the lowest AIC score corrected for small sample sizes (AIC$_c$, Burnham and Anderson 1998) was determined to be the model best fitting the data.

Complete separation of data points occurred with the full model for Western Meadowlark. Therefore I performed a forward selection procedure and considered the full model to include all variables entered into the model up to the point where complete separation occurred. The same model selection procedure outlined above was then used to identify the most parsimonious models.

Nest-survival models. I used the logistic exposure method (Shaffer 2004) to determine whether nest survival was influenced by nest age, date, or year effects. I only included nests that were determined to be either successful or depredated. Nests that failed for other reasons (e.g., cattle trampling, weather, etc.) were excluded. *A priori* models I considered included linear effects of age and date, quadratic effects of age and date, cubic effect of age, a null (constant survival) model, and a global model. I considered models with and without year effects for a total of 20 models. Quadratic models included both linear (x) and quadratic (x^2) terms while cubic models included linear, quadratic, and cubic terms (x^3). I used the effective sample size (Rotella et al. 2004) to calculate AIC$_c$ and evaluated the models.

In addition, I determined whether nest vegetation was a good predictor of nest survival by using the same backward elimination procedure on vegetation factors described above for nest-site selection models. I included nest concealment with vegetation factors in the full model. I then compared AIC$_c$ values from the following seven models, 1) null, 2) the best nest survival model without vegetation variables (i.e., only age, date, and year effects), 3) the best nest survival model comprising only vegetation variables, 4) the best nest survival model with age or date effects and vegetation variables, 5) a model containing vegetation variables from the best nest-site selection model, 6) the best nest survival model with vegetation variables from the best nest-site selection model, and 7) a global model. This comparison allowed me to, 1) determine whether nest vegetation explained additional variation not accounted for age, date, or year effects and 2) whether nest-site features associated with increased nest survival shared similar characteristics as microhabitat features important in nest-site selection.

RESULTS

NEST-SITE SELECTION

Vegetation was quantified at 562 nests over the four years of the study. Chestnut-collared Longspur nests dominated the sample ($n = 251$), followed by Baird's Sparrow ($n = 120$), Western Meadowlark ($n = 68$), Sprague's Pipit ($n = 62$), and Savannah Sparrow ($n = 61$).

Examination of the best nest-site selection models indicated that model selection uncertainty was high and thus model averaging was employed for Chestnut-collared Longspur, Savannah Sparrow, Baird's Sparrow, and Sprague's Pipit. The Western Meadowlark model did not converge after the sixth variable entered the model due to complete separation of data points. Subsequently the global model comprised six parameters (including intercept) and had an AIC$_c$ weight of 0.98. Thus parameter estimates and standard errors were used from this model. Overall, 9 of 10 factors were included in models with a ΔAIC$_c < 7$. The only factor not included

TABLE 1. Model-averaged parameter estimates and unconditional standard errors for vegetation factors from principal components analyses that were included in nest-site selection models for five grassland passerines. Asterisks indicate model parameters with 90% confidence limits that do not include zero. Dashes indicate variables that were not included in any of the models.

Vegetation factor	Sprague's Pipit ($n = 62$)[a]	Savannah Sparrow ($n = 61$)	Baird's Sparrow ($n = 120$)	Chestnut-collared Longspur ($n = 251$)	Western Meadowlark ($n = 68$)
Density of live grasses >30 cm	–	1.74 ± 1.92	1.83 ± 0.78*	0.14 ± 0.38	8.63 ± 4.64*
Density of dead vegetation <30 cm	2.54 ± 0.74*	2.23 ± 0.97*	1.37 ± 0.36*	1.35 ± 0.32*	6.34 ± 2.69*
Density of forbs ≥50 cm	−1.04 ± 0.82	−5.80 ± 3.21	0.07 ± 0.16	−0.39 ± 0.64	35.80 ± 19.01*
Density of live grasses <30 cm	–	1.71 ± 1.17	0.63 ± 0.51	0.90 ± 0.30*	–
Density of shrubs & forbs 20–39 cm	−1.68 ± 1.01	0.79 ± 0.92	0.50 ± 0.40	0.08 ± 0.31	6.54 ± 3.33*
Density of dead vegetation ≥30 cm	2.17 ± 2.81	−0.41 ± 1.45	0.16 ± 0.27	0.81 ± 0.68	–
Increased litter depth, decreased bare ground	1.13 ± 0.76	1.40 ± 0.80*	1.90 ± 0.51*	1.63 ± 0.34*	1.46 ± 1.09
Distance to nearest shrub	2.44 ± 1.30*	−2.12 ± 1.28*	1.32 ± 0.59*	0.92 ± 0.37*	–
Cow dung cover	0.63 ± 0.64	1.54 ± 0.77*	−0.62 ± 0.66	0.76 ± 0.17*	–

[a] n = number of nests.

in the models represented a high density of forbs within 10 cm of the ground. Despite the inclusion of most vegetation factors, unconditional standard errors were large for many parameters (Table 1). Factor 2, representing the density of dead vegetation within 30 cm of the ground, was positively associated with nest sites and was included in the best model for each species (Table 1). Factor 7, representing sites with increased litter depth and reduced coverage of bare ground, was the only other variable included in the best model for each species. Nest sites were positively associated with this variable but standard errors were relatively large except for Baird's and Savannah sparrows and Chestnut-collared Longspur (Table 1). Nest sites of grassland specialists such as pipits, longspurs and Baird's Sparrows were located in sites where shrubs were sparse. However, Baird's Sparrow nest sites differed by having greater densities of tall live and dead grasses (Table 1). Meadowlarks were the only species strongly associated

with sites that had greater densities of tall shrubs and forbs and Savannah Sparrows and longspurs were the only species strongly associated with sites with a greater coverage of cow dung (Table 1). In addition, Chestnut-collared Longspur nests were more visible than those of other species', whereas the domed nests of Sprague's Pipit and Western Meadowlark were most concealed (Fig. 1). The exposed nature of longspur nests was partly due to nest sites having lower densities of standing dead vegetation and shorter vegetation than other species (Fig. 1). In addition, Chestnut-collared Longspur nest sites had more bare ground and less litter than most species' nests (Fig. 1).

Canonical discriminant analysis separated species based on nest vegetation variables (F_{64} = 6.3, $P < 0.001$) and supported the findings above. Species were separated along the first canonical axis representing a gradient from short, sparse vegetation and greater coverage of bare ground to sites comprised of increased densities
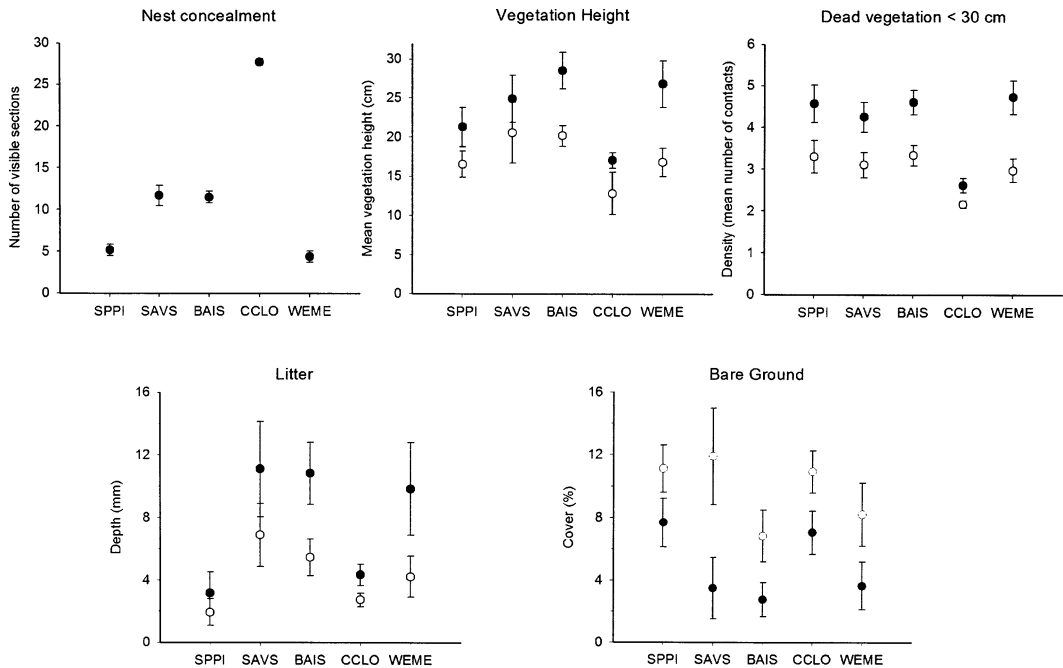
FIGURE 1.   Mean (± 95% CI) values for nest concealment and vegetation features from nest and random sites for Sprague's Pipit (SPPI, $n = 63$), Savannah Sparrow (SAVS, $n = 62$), Baird's Sparrow (BAIS, $n = 123$), Chestnut-collared Longspur (CCLO, $n = 266$), and Western Meadowlark (WEME, $n = 73$). Black and white circles represent nest and random sites, respectively.
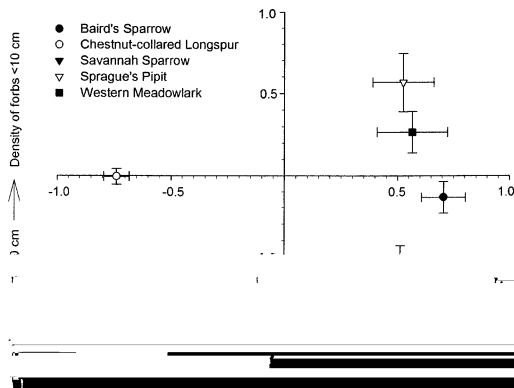

FIGURE 2.   Separation of grassland songbird nest sites along a vegetation gradient. The first canonical axis represents a gradient from short, sparse vegetation and greater coverage of bare ground to vegetation comprised of increased densities of standing dead vegetation and tall grasses, and greater litter depth. The second canonical axis represents a gradient from a high density of forbs 10–20 cm in height (negative values) to a high density of forbs <10 cm tall. Symbols are means (± SE) of factor scores.

of standing dead vegetation and tall grasses, and greater litter depth (Fig. 2). Chestnut-collared Longspurs nests were associated with sites characterized by shorter and more sparse vegetation whereas the other species' nest sites were associated with taller and thicker cover (Fig. 2). The second canonical axis represents a gradient of sites with increased density of forbs 10–20 cm tall to sites with a high density of forbs within 10 cm of the ground (Fig. 2). Savannah Sparrow, Sprague's Pipit, and Western Meadowlark nests occupied sites towards the extremes of this gradient, while Baird's Sparrow and Chestnut-collared Longspur nests occupied intermediate sites (Fig. 2).

NEST SURVIVAL

Nest survival was not constant over the nesting period for any species (Table 2). Nest survival for Sprague's Pipit, Savannah Sparrow, and Chestnut-collared Longspur was best explained by a linear effect of age with nest survival decreasing with the age of the nest. A cubic effect of age best explained Baird's Sparrow and Western Meadowlark nest survival (Table 2). Nest

TABLE 2.   Nest survival models for five mixed-grass prairie passerines. Models include the best model (lowest AIC_c value), candidate models within 2 AIC_c units from best model, and null (constant survival) models. The number of parameters (k) and AIC_c weights (w_i) for each model are provided. Global models include linear, quadratic, and cubic effects of age, linear and quadratic effects of date, age by date interaction, and year.

Species	Model	k	AIC_c	ΔAIC_c	w_i
Sprague's Pipit (n^a = 677)					
	Year–Age	5	270.7	0.0	0.35
	Year + Age^2	6	272.7	2.0	0.13
	Year–Age + Date	6	272.7	2.0	0.13
	Constant survival	1	276.8	6.1	0.02
Savannah Sparrow (n = 344)					
	Year–Age–Date	5	172.8	0.0	0.28
	Year–Age–Date + Age*Date	6	174.1	1.3	0.15
	Year–Age	4	174.4	1.6	0.14
	Constant survival	1	181.0	8.2	0.00
Baird's Sparrow (n = 928)					
	Age^3	4	456.0	0.0	0.36
	Age^3 + Date	5	457.0	1.0	0.22
	Age^3 + $Date^2$	6	457.7	1.7	0.15
	Constant survival	1	462.9	6.9	0.01
Chestnut-collared Longspur (n = 1921)					
	–Age	2	960.2	0.0	0.21
	Age^3	4	961.4	1.2	0.11
	–Age + Date	3	961.8	1.6	0.09
	–Age + Year	4	962.0	1.8	0.08
	Age^2	3	962.2	2.0	0.07
	Constant survival	1	963.9	3.7	0.03
Western Meadowlark (n = 510)					
	Age^3 + Date + Year	7	249.4	0.0	0.26
	Age^3 + $Date^2$	6	249.5	0.1	0.23
	Age^3 + $Date^2$ + Year	8	249.8	0.4	0.21
	Age^3 + Date	5	250.6	1.2	0.14
	Constant survival	1	261.5	12.1	0.00

[a] n = Number of intervals.

survival increased during laying and through early incubation, dropped after hatching, and increased as the young aged. Date effects were present in the best or candidate models of all species with nest survival increasing with date for all species except Savannah Sparrows (Table 2).

Comparisons of the best nest-survival models composed only of vegetation variables with null models indicated that nest vegetation influenced survival of grassland passerine nests. With the exception of Western Meadowlark, survival models containing only vegetation variables outperformed null models (ΔAIC_c > 2) . Furthermore, nest-survival models including only age or date effects had higher AIC values ($\Delta AIC_c \geq$ 3) than models composed of both age or date effects and vegetation variables. Although vegetation structure was an important predictor of

nest survival for most species, it was extremely variable as all 90% confidence limits overlapped with zero for each species except Sprague's Pipit (Table 3).

DISCUSSION

Grassland songbirds in this study exhibited nonrandom nest-placement patterns. I found that each grassland species nested in sites that were characterized by a greater density of dead vegetation within 30 cm of the ground, increased amounts of litter, and reduced coverage of bare ground. In addition, each species nested in taller vegetation than that found at random sites.

Although the five species I studied selected sites with a greater density and height of nesting cover, Chestnut-collared Longspur nests were more exposed than other species. In addition, density and height of vegetation in the area with-

TABLE 3.   Model-averaged parameter estimates and unconditional standard errors for variables included in nest survival models for five grassland passerines. Variables include vegetation factors from principal components analyses, nest visibility, linear effects of age and date, quadratic and cubic effects of age, and year effects. Asterisks indicate model parameters with 90% confidence limits that do not include zero and dashes indicate variables that were not included in any of the models.

Parameter	Sprague's Pipit (n^a = 677)	Savannah Sparrow (n = 344)	Baird's Sparrow (n = 928)	Chestnut-collared Longspur (n = 1921)	Western Meadowlark (n = 510)
Density of live grasses >30 cm	0.02 ± 0.05	–	−0.00 ± 0.01	–	0.00 ± 0.01
Density of dead vegetation <30 cm	0.00 ± 0.01	−0.02 ± 0.04	−0.02 ± 0.04	0.00 ± 0.01	−0.00 ± 0.01
Density of forbs ≥50 cm	–	−0.04 ± 0.09	–	–	−0.17 ± 0.33
Density of live grasses <30 cm	0.29 ± 0.30	0.14 ± 0.21	0.21 ± 0.14	0.00 ± 0.01	0.03 ± 0.07
Density of shrubs & forbs 20–39 cm	0.01 ± 0.04	0.31 ± 0.29	–	–	−0.00 ± 0.01
Density of dead vegetation ≥30 cm	1.44 ± 1.07	–	–	–	–
Increased litter depth, decreased bare ground	−0.01 ± 0.02	0.00 ± 0.01	−0.01 ± 0.02	−0.00 ± 0.01	0.03 ± 0.07
Density of forbs <10 cm and dwarf shrubs	–	0.51 ± 0.46	–	–	–
Distance to nearest shrub	0.81 ± 0.33*	0.01 ± 0.03	0.00 ± 0.00	0.00 ± 0.01	–
Cow dung cover	−0.54 ± 0.27*	0.00 ± 0.02	–	0.00 ± 0.00	–
Nest visibility	–	−0.00 ± 0.00	–	0.02 ± 0.01	–
Age	−0.09 ± 0.04*	−0.14 ± 0.05*	0.97 ± 0.39*	−0.03 ± 0.01	1.28 ± 0.39*
Age^2	–	–	−0.07 ± 0.03*	–	−0.08 ± 0.03*
Age^3	–	–	0.00 ± 0.00*	–	0.00 ± 0.00*
Date	–	0.02 ± 0.01	–	–	0.03 ± 0.01
1997	−0.85 ± 0.67	−0.12 ± 0.67	–	–	−0.31 ± 0.52
1998	0.39 ± 0.45	0.92 ± 0.84	–	–	−0.91 ± 0.51*
1999	0.32 ± 0.67	0	–	–	0
Intercept	4.34 ± 0.91	1.58 ± 2.59	−1.48 ± 1.50	3.57 ± 0.53	−7.71 ± 2.55

[a] n = number of intervals.

in 30 m of longspur nests were much lower compared to other species. Thus longspurs nested in areas with shorter and sparser vegetation compared to other species, but selected nesting sites with taller and denser vegetation within these areas. Another unique feature of longspur nests was their association with cow dung. Indeed, 42% of 299 longspur nests in this study were adjacent to cow dung, similar to the proportion (43% of 23 nests) reported by Harris (1944). Although the function of this nest site attribute is currently unknown (Hill and Gould 1997), it may assist in concealing the nest or attending adult. Cow dung and other objects (e.g., rocks, grass clumps) may also influence

the microclimate of the nest by reducing exposure to wind and sun (Nelson and Martin 1999, Hartman and Oring 2003). Savannah Sparrow nests were also associated with cow dung, but the nest sites were much different than longspur nest sites. In nearly all cases where cow dung was recorded, Savannah Sparrow nests were located near old pieces of decayed cow dung, not directly adjacent to the dried-out, but intact pats that were found adjacent to longspur nests. Savannah Sparrows may have chosen these sites because of the thick vegetation growth associated with them.

Grassland passerines incur high nest predation rates (Martin 1993). In my study, nest success

estimates ranged from 14% to 24% with 88% of unsuccessful nests attributed to predators (Davis 2003b). Thus selection pressures should lead grassland passerines to place their nests in safe places (Martin 1992). In this study, nesting in areas composed of taller, thicker vegetation with reduced coverage of bare ground may reduce predation risk by providing increased concealment for the nest and attending adult. Because nest vegetation was measured after the nesting attempt had terminated, it is difficult to ascertain whether the relationship between nest survival and concealing vegetation is an artifact of successful nests surviving longer into the growing season. For example, date effects were included in the best survival model for Western Meadowlark with nest survival increasing with date. Although not included in the best models, date effects were present in the candidate models for the other species and with the exception of Savannah Sparrow, nest survival increased with date. The fact that all species selected sites with taller and thicker cover than what was available suggests that management regimes should ensure that adequate cover is available to these species during the breeding season, regardless of whether nest survival increases as the breeding season progresses because of growing vegetation, changes in predator populations, or any other factors not measured or currently understood.

If the amount of vegetation concealing the nests is positively associated with nest survival, why do mixed-grass prairie passerines not select sites with the tallest and most dense vegetation available? Nest sites and territories of grassland passerines were partitioned along a vegetation gradient ranging from relatively short and sparse (e.g., Chestnut-collared Longspur) to relatively tall and dense vegetation (e.g., Baird's Sparrow and Western Meadowlark). Such partitioning could result from interspecific competition (Svardson 1949, but see Wiens 1985, Zimmerman 1992). Longspurs, for example, may occupy areas with shorter, sparser vegetation because they are excluded from sites with more cover. However, this does not seem likely as Chestnut-collared Longspurs reach their highest abundance in grasslands that are grazed and disappear from sites that are not periodically disturbed (Hill and Gould 1997, Johnson et al. 1998). The tallest and most densely vegetated sites may not be selected for by all species be-

cause of a trade-off between concealing the nest with the need for vigilance and quick escape due to predation risk (Gotmark et al. 1995). Alternatively, partitioning of nest sites may result from grassland birds selecting nests sites that differ from co-existing species to reduce the likelihood of predation (Martin 1996). Native mixed-grass prairie, particularly lightly and moderately grazed pastures (as in this study), are structurally heterogeneous, and thus if birds only locate nests where vegetation is tall and dense, predators may be better able to develop effective search strategies. In addition, many nest predators are prey themselves and seek cover for protection; thus, longspurs may select nest sites in areas with shorter and sparser cover to avoid smaller predators that rely on cover to escape predation. This may account for longspurs' relatively high nest success compared to other species in 1997 when nest predation was either directly or indirectly influenced by extremely high vole numbers (Davis 2003b).

Although models containing vegetation variables were better predictors of nest survival than models without vegetation variables, these patterns do not necessarily indicate that nest-site selection is adaptive from the perspective of reducing risk of predation, as some individuals may be prevented from occupying high-quality sites (Petit and Petit 1996, Martin 1998). In addition, vegetation parameters were highly variable. A number of nonexclusive hypotheses have been advanced to explain why nest-site features might not appear to influence predation risk. Filliater et al. (1994) postulated that diverse predator assemblages make it difficult for birds to select optimal nest sites because of different search strategies and sensory cues predators used to locate nests. Grassland passerines are exposed to a wide array of predators (Pietz and Granfors 2000, Renfrew and Ribic 2003), such that optimal nest-site features may be unpredictable. Furthermore, most predators of grassland songbird nest are generalists that may opportunistically prey on nests found during foraging bouts for preferred prey (Vickery et al. 1992, Cooper et al. 1999).

Several authors have suggested that spatial and temporal variation in selective pressures may explain why preferred microhabitats do not appear adaptive (Clark and Shutler 1999, Misenhelter and Rotenberry 2000). For example, anthropogenic changes to grassland habitat may

have occurred too quickly for many bird species to adapt (e.g., time-lag effects, Wiens 1985). Furthermore, predation pressure has been found to fluctuate dramatically in grasslands (Clark and Shutler 1999, Davis 2003b), thus nest-site selection may reflect optimal conditions that are adaptive over time, but appear to be neutral or maladaptive in the short term (Wray and Whitmore 1979, Clark and Shutler 1999). Indeed, predation frequency varied greatly for most species during this study and was over three times higher for some passerines in 1997, when voles (*Microtus* spp.) experienced a dramatic population increase (Poulin et al. 2001, Davis 2003b). It is reasonable to assume that the predictability of optimal nest-site features would be low because of the sudden increase in voles and avian predators during this event (Poulin et al. 2001). Reproductive success may also be affected directly by weather conditions (George et al. 1992, Fernandez and Reboreda 1998), or indirectly by weather influencing the physiology and behavior of predators and their prey, and the interaction between them (Schmidt 1999).

The results of my study reveal strong nest-site selection patterns within species and provide limited support to the contention that predation influences nest-site choice in grassland birds. Rather, time-specific factors such as nest age appear to be a stronger predictor of nest survival. Interestingly, Grant et al. (2005) also found strong age effects for two grassland passerines in North Dakota. Furthermore, their best models included a cubic effect of age, similar to my findings for Baird's Sparrow, Western Meadowlark, and Chestnut-collared Longspur. Although more studies are required, these results suggest this pattern may be common among grassland passerines. Despite the stronger influence of age on nest survival, the apparent preference for nest sites with taller and denser cover by all species in this study should provide reproductive benefits to breeding birds over time as concealed sites would likely offer more protection from visual predators than exposed sites (Liebezeit and George 2002), assuming that predation by predators that do not rely on visual cues is not greater for concealed nests. Clearly, more studies are required to determine the adaptive significance of nest-site selection in grassland birds and uncover the mechanisms that are driving the observed patterns.

LITERATURE CITED

BEST, L. B., H. CAMPA, K. E. KEMP, R. J. ROBEL, M. R. RYAN, J. A. SAVIDGE, H. P. WEEKS, AND S. R. WINTERSTEIN. 1997. Bird abundance and nesting in CRP fields and cropland in the Midwest: a regional approach. Wildlife Society Bulletin 25: 864–877.

BOWMAN, G. B., AND L. D. HARRIS. 1980. Effect of spatial heterogeneity on ground-nest depredation. Journal of Wildlife Management 44:806–813.

BURNHAM, K. P., AND D. R. ANDERSON. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.

CLARK, R. G., AND D. SHUTLER. 1999. Avian habitat selection: pattern from process in nest site use by ducks? Ecology 80:272–287.

COOPER, R. J., R. R. WILSON, G. D. ZENITSKY, S. J. MULLIN, J. A. DECECCO, M. R. MARSHALL, S. J. WOLF, AND L. Y. POMARA. 1999. Does nonrandom nest placement imply nonrandom nest predation?

the conservation of North American passerine birds. University of Texas Press, Austin, TX.

FERNÁNDEZ, G. J., AND J. C. REBOREDA. 1998. Effects of clutch size and timing of breeding on reproductive success of Greater Rheas. Auk 115:340–348.

FILLIATER, T. S., R. BREITWISCH, AND P. M. NEALEN. 1994. Predation on Northern Cardinal nests: does choice of nest site matter? Condor 96:761–768.

GEORGE, T. L., A. C. FOWLER, R. L. KNIGHT, AND L. C. MCEWEN. 1992. Impacts of a severe drought on grassland birds in western North Dakota. Ecological Applications 2:275–284.

GOTMARK, F, D. BLOMQVIST, O. C. JOHANSSON, AND J. BERGKVIST. 1995. Nest site selection: a trade-off between concealment and view of the surroundings? Journal of Avian Biology 26:305–312.

GRANT, T. A., T. L. SHAFFER, E. M. MADDEN, AND P. J. PIETZ. 2005. Time-specific variation in passerine nest survival: new insights into old questions. Auk 122, in press.

HARRIS, R. D. 1944. The Chestnut-collared Longspur in Manitoba. Wilson Bulletin 56:105–115.

HARTMAN, C. A., AND L. W. ORING. 2003. Orientation and microclimate of Horned Lark nests: the importance of shade. Condor 105:158–163.

HERKERT, J. R. 1994. The effects of habitat fragmentation on midwestern grassland bird communities. Ecological Applications 4:461–471.

HILL, D. P., AND L. K. GOULD. 1997. Chestnut-collared Longspur (*Calcarius ornatus*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 288. The Academy of Natural Sciences, PA, and The American Ornithologists' Union, Washington, DC.

JOHNSON, D. H., AND M. D. SCHWARTZ. 1993. The Conservation Reserve Program: habitat for grassland birds. Great Plains Research 3:273–295.

JOHNSON, D. H., L. D. IGL, J. A. DECHANT, M. L. SONDREAL, C. M. GOLDADE, M. P. NENNEMAN, AND B. R. EULISS. 1998. Effects of management practices on grassland birds: Chestnut-Collared Longspur. Northern Prairie Wildlife Research Center, Jamestown, ND.

KOFORD, R. R. 1999. Density and fledging success of grassland birds in Conservation Reserve Program fields in North Dakota and west-central Minnesota. Studies in Avian Biology 19:187–195.

LIEBEZEIT, J. R., AND T. L. GEORGE. 2002. Nest predators, nest-site selection and nesting success of the Dusky Flycatcher in a managed ponderosa pine forest. Condor 104:507–517.

MADDEN, E. M., R. K. MURPHY, A. J. HANSEN, AND L. MURRAY. 2000. Models for guiding management of prairie bird habitat in northwestern North Dakota. American Midland Naturalist 144:377–392.

MARTIN, T. E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management, p. 455–473. *In* J. M. Hagen III and D. W. Johnston [EDS.], Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, DC.

MARTIN, T. E. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. American Naturalist 141:897–913.

MARTIN, T. E. 1996. Fitness costs of resource overlap among coexisting bird species. Nature 380:338–340.

MARTIN, T. E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive. Ecology 79:656–670.

MISENHELTER, M. D., AND J. T. ROTENBERRY. 2000. Choices and consequences of habitat occupancy and nest site selection in Sage Sparrows. Ecology 81:2892–2901.

NELSON, K. J., AND K. MARTIN. 1999. Thermal aspects of nest-site location for Vesper Sparrows and Horned Larks in British Columbia. Studies in Avian Biology 19:137–143.

PETIT, L. J., AND D. R. PETIT. 1996. Factors governing habitat selection by Prothonotary Warblers: field tests of the Fretwell-Lucas models. Ecological Monographs 66:367–387.

PIETZ, P. J., AND D. A. GRANFORS. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. Journal of Wildlife Management 64:71–87.

POULIN, R. G., T. I. WELLICOME, AND L. D. TODD. 2001. Synchronous and delayed numerical responses of a predatory bird community to a vole outbreak on the Canadian prairies. Journal of Raptor Research 35:288–295.

RENFREW, R. B., AND C. A. RIBIC. 2003. Grassland passerine nest predators near pasture edges identified on videotape. Auk 120:371–383.

ROTELLA, J. J., S. J. DINSMORE, AND T. L. SHAFFER. 2004. Modelling nest survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. Animal Biodiversity and Conservation 27:1–19.

ROTENBERRY, J. T., AND J. A. WIENS. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61:1228–1250.

SAS INSTITUTE, INC. 1999. SAS online document, ver. 8. SAS Institute Inc, Cary, NC.

SCHMIDT, K. A. 1999. Foraging theory as a conceptual framework for studying nest predation. Oikos 85:151–160.

SHAFFER, T. L. 2004. A unified approach to analyzing nest success. Auk 121:526–540.

SUTTER, G. C. 1997. Nest-site selection and nest-entrance orientation in Sprague's Pipit. Wilson Bulletin 109:462–469.

STOKES, M. E., C. S. DAVIS, AND G. G. KOCH. 2000. Categorical data analysis using the SAS system, second edition. SAS Institute, Cary, NC.

SVARDSON, G. 1949. Competition and habitat selection in birds. Oikos 1:157–174.

VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

TASK GROUP ON UNITY IN CONCEPTS AND TERMINOLOGY. 1995. New concepts for assessment of rangeland

condition. Journal of Range Management 48:271–282.

VICKERY, P. D., M. L. HUNTER JR., AND J. V. WELLS. 1992. Is density an indicator of breeding success? Auk 109:706–710.

WIENS, J. A. 1985. Habitat selection in variable environments: shrub-steppe birds, p. 227–251. *In* M. L. Cody [ED.], Habitat selection in birds. Academic Press, Orlando, FL.

WINTER, M. 1999. Nesting biology of Dickcissels and Henslow's Sparrows in southwestern Missouri prairie fragments. Wilson Bulletin 111:515–527.

WITH, K. A., AND D. R. WEBB. 1993. Microclimate of ground nests: the relative importance of radiative cover and wind breaks for three grassland species. Condor 95:401–413.

WITH, K. A. 1994. The hazards of nesting near shrubs for a grassland bird, the McCown's Longspur. Condor 96:1009–1019.

WRAY, T., AND R. C. WHITMORE. 1979. Effects of vegetation on nesting success of Vesper Sparrows. Auk 96:802–805.

ZIMMERMAN, J. L. 1992. Density-independent factors affecting the avian diversity of the tallgrass prairie community. Wilson Bulletin 104:85–94.