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LARK SPARROW (*CHONDESTES GRAMMACUS*) NEST-SITE SELECTION AND SUCCESS IN A MIXED-GRASS PRAIRIE

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ABSTRACT.—Lark Sparrows (*Chondestes grammacus*) are declining throughout most of their range. Effective management for this species is hampered because relatively little is known about nesting ecology. We studied habitat characteristics affecting Lark Sparrow nest-site selection and nest success at nine study pastures in a southern mixed-grass prairie in Oklahoma. We used a neural-network technique to discriminate between nest and random locations, and bootstrapping with 95% confidence intervals to compare habitat features of successful and unsuccessful nests. We quantified habitat features at the nest and random points during the breeding seasons of 1999 and 2000 among three grazing treatments (control, moderate, and heavy). We located 40 nests during two years of the study, for which crude nest-success was 26.3%. Most nests were located in either moderately grazed pasture (55%) or heavily grazed pasture (40%). The neural model correctly identified nest and random points 91% of the time. Percentage of structural cover, distance to nearest structural element, bare-ground exposure, and percentage of litter cover were the most important nest-site selection criteria according to the model. Simulation analysis indicated points were classified as nest sites if they were <270 cm from structural elements, <87% bare-ground exposure, <74% litter cover, and >9% structural cover. Successful nests had less bare-ground exposure ($\bar{x}$ = 6.2 ± 1.9% [SE]) and more litter cover ($\bar{x}$ = 18.0 ± 4.6%) compared to unsuccessful nests ($\bar{x}$ = 17.5 ± 3.8% and 10.1 ± 1.6%, respectively). These results suggest that habitat management for Lark Sparrows in mixed-grass prairie should focus on creating abundant structural cover with moderate levels of litter accumulation and bare ground. *Received 4 February 2002, accepted 12 September 2002.*

RESUMEN.—Las poblaciones de *Chondestes grammacus* están disminuyendo a través de una gran parte de su rango de distribución. El manejo efectivo para esta especie se ve impedido debido al escaso conocimiento de su biología reproductiva. Estudiamos las características del hábitat que afectan la selección de los sitios de nidificación en nueve pastizales en una pradera de pastos mixtos del sur en Oklahoma. Utilizamos una técnica de redes neurales para discriminar entre los sitios de los nidos y sitios al azar, y la técnica de "bootstrapping" con un 95% de intervalo de confianza para comparar las características de los hábitats con nidos exitosos y con nidos no exitosos. Cuantificamos las características del hábitat en los sitios de los nidos y en puntos al azar durante las épocas reproductivas de 1999 y 2000 entre tres tratamientos de pastoreo (control, moderado e intenso). Localizamos 40 nidos durante los dos años de estudio, para los cuales el éxito crudo fue del 26.3%. La mayoría de los nidos se encontró en las praderas con pastoreo moderado (55%) o en las praderas con pastoreo intenso (40%). El 91% de las veces el modelo neural identificó correctamente los sitios de los nidos y los puntos al azar. Según el modelo, el porcentaje de cobertura estructural, la distancia al elemento estructural más cercano, la exposición de suelo desnudo y el porcentaje de cubierta de hojarasca fueron los criterios más importantes para la selección del sitio del nido. Análisis de simulaciones indicaron que los puntos fueron clasificados como sitios de nido si se encontraban a <270 cm de elementos estructurales, si presentaban <87% de exposición de suelo descubierto, <74% de cubierta de hojarasca, y >9% de cubierta estructural. Los nidos exitosos tuvieron menor exposición de suelo descubierto ($\bar{x}$ = 6.2 ± 1.9% [EE]) y cobertura de hojarasca ($\bar{x}$ = 18.0 ± 4.6%) en comparación con los nidos no exitosos ($\bar{x}$ = 17.5 ± 3.8% and 10.1 ± 1.6%, respectivamente). Estos resultados sugieren que el manejo del hábitat para *C. grammacus* en las praderas de pastos mixtos debería enfocarse en crear abundante cobertura estructural con niveles moderados de acumulación de hojarasca y suelo descubierto.

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LITTLE IS KNOWN about the breeding ecology of Lark Sparrows (*Chondestes grammacus*; Martin and Parrish 2000). Available information on Lark Sparrow nest-site selection is limited to descriptive studies conducted in the southern Great Plains (Newman 1970, Walcheck 1970, Renwald 1977, McNair 1984, Suedkamp 2000). Martin and Parrish (2000) reported that most nests were located on bare ground, sometimes in a small depression located at the base of woody plants. However, in some portions of their range, Lark Sparrows also nest in trees and shrubs (Martin and Parrish 2000). Further information regarding vegetation composition and structure of nest sites has not been well documented to date (Suedkamp 2000), nor has the relationship between nest-site location and nest success been evaluated.

Lark Sparrow populations are declining by 3% annually across their range in North America and have declined by 61.2% between 1966 and 1993 (Sauer et al. 1997). Declines are greatest in the eastern and central regions of the Breeding Bird Survey (Sauer et al. 1997, Martin and Parrish 2000). In Oklahoma and Texas, where breeding densities are among the highest in the United States, Lark Sparrows are declining at 3.5% per year and 4.2% per year, respectively (Sauer et al. 1997).

Nest placement will often influence the risk of nest predation (Ricklefs 1969, Martin 1993) and the microclimate experienced during incubation (With and Webb 1993, Gloutney and Clark 1997, Nelson and Martin 1999), thus affecting the ultimate fate of the nesting attempt. Therefore, the selection of a nest site is crucial to the fitness of the breeding pair, and natural selection should strongly influence the nest-site selection process.

Our objectives were twofold: first, we determined nest-site characteristics for Lark Sparrows and evaluated the effect of those characteristics on nesting success. Such knowledge will provide researchers with a better understanding of the breeding ecology of this species and might help elucidate potential causes of the species' decline. We also compared habitat features between successful and unsuccessful nests to determine how those habitat characteristics influenced Lark Sparrow nest success; second, we evaluated various hypotheses regarding nest-site selection behavior proposed to explain patterns of nest-site locations. To those ends, we employed a relatively new method of analysis called "artificial neural networks" (Smith 1996). We used that approach to compare features between nest sites and random points, and then used bootstrapping to investigate variables that were most important to the neural model in distinguishing successful from unsuccessful nests.

METHODS

We collected nest-site selection and success data at the Marvin Klemme Experimental Range Research Station (35°25'N, 99°05'W) in western Oklahoma, near Bessie in Washita County. The research station is located in the southern mixed-grass prairie physiographic region (Coupland 1992). Dominant vegetation on the site includes sideoats grama (*Bouteloua curtipendula*), purple threeawn (*Aristida purpurea*), western ragweed (*Ambrosia psilostachya*), common broomweed (*Amphiachyris dracuncloides*), smooth sumac (*Rhus glabra*), and broom snakeweed (*Guiterrezia sarothrae*).

Individual pastures at the station are managed under three grazing treatments: (1) no grazing ($\geq$50 years), (2) moderate grazing (0.2 animal units per ha), and (3) heavy grazing (0.4 animal units per ha). The no-grazing treatment consisted of one, 16 ha pasture. Moderate and heavy treatments consisted of four pastures each. Moderately grazed pastures varied in size between 40.8 and 57.7 ha, whereas heavily grazed pastures ranged between 39.5 and 46.0 ha. Stocker cattle occupied the pastures for five consecutive months (April–August) of each year.

We randomly selected three pastures in both the moderate and heavy grazing treatments for measuring habitat variables, and randomly established 1 ha plots using an existing array of stakes 100 m apart. In the ungrazed pasture, we established three, 1 ha plots. We had nine sampling plots (3 plots per treatment × 3 treatments = 9 sample plots) each containing 10 randomly established permanent points for a total of 90 sampling points (9 plots × 10 points per plot = 90 points). Those random points were selected by generating random x and y coordinates and using the northwest corner of each plot as the origin. Jones and Robertson (2001) found that for Cerulean Warblers (*Dendroica cerulea*) random points outside of the nesting territory might not adequately represent the habitat available for nest-site selection. However, Lark Sparrows are not territorial and defend only the immediate nest site (Martin and Parrish 2000). Therefore, we used these random sampling-points to measure the habitat available to Lark Sparrows for nest sites during the summers of 1999 and 2000.

We searched for nests from the beginning of May through early July in 1999 and 2000, employing systematic searches and random walks through each sample pasture. Once a nest was located, it was

marked ≥5 m away from the nest in two directions. Nests were then monitored every three to four days until fledging, abandonment, or depredation. We did not attempt to determine the identity of nest predators because of concerns over the possible misidentification of predators (Larivière 1999).

Habitat features were measured at all points at the beginning of the growing season in May and at the end of the growing season in late July and early August. Vegetation changes over the growing season varied depending on the timing and amount of precipitation (Suedkamp 2000). We measured litter depth (millimeters), distance to visual obstruction (meters), screening cover (percentage), tallest plant height (centimeters), distance to nearest structural element (centimeters), structural cover (percentage), bare-ground exposure (percentage), litter cover (percentage), and species composition (percentage, grass and forb). We defined structural elements as any plant that provided nesting structure similar to woody plants, regardless of whether it is woody or herbaceous. Species in that category included broom snakeweed, common broomweed, and smooth sumac. We followed the Robel et al. (1970) method of measuring visual obstruction and the Nudds (1977) method for measuring screening cover. For our analyses of screening cover, we used the mean cover class of the second through the fifth strata based on the midpoint of each cover class. We quantified the distance to nearest structural element and structural cover using the point-centered quarter method (Cottam et al. 1953). We measured the remaining habitat and species composition variables using a 2 × 5 decimeter frame (Daubenmire 1959) placed immediately north of each sampling point. At the end of both breeding seasons, we measured the same variables at nest and random points concurrently. We used those end-of-season measurements in the model. Most structural variables were measured in the same manner as at random sampling points, except for tallest plant height, bare-ground exposure, litter cover, and species composition variables that were measured by centering the frame on the nest rather than to its direct north.

Artificial neural network models are a type of machine-learning algorithm (Smith 1996, Fielding 1999a). They are well suited to learning patterns in large, noisy multivariate data sets. As a result, the use of neural network models has been increasing in ecology (Colasanti 1991, Edwards and Morse 1995). Neural networks have been used to model algal blooms (Recknagel et al. 1997, Maier et al. 1998), tallgrass prairie biomass (Olson and Cochran 1998), presence of small-bodied fish in rivers (Mastrorillo et al. 1997), and abundance of Northern Bobwhites (*Colinus virginianus*) (Lusk et al. 2001). Neural network models are nonparametric; they can model both linear and nonlinear relationships without *a priori* specification of the form of the relationship; they are unaffected by multicollinearity; and they can be applied to prediction and discrimination problems (Smith 1996). However, due to the structure of the neural network model, interpretation of the model output is not straightforward and requires additional simulation modeling to elucidate biologically meaningful results.

We used a neural network model that consisted of three layers, each containing a series of nodes that represent various components of the model (Smith 1996). The first layer, called the input layer, contained nodes representing each independent variable. The second layer, called the neuron layer, contained processing elements that attempt to predict the dependent variable represented in the third layer. Nodes in the neuron layer apply weights to the values of the independent variables, sums them, and then transforms them using one of several transfer functions (Smith 1996). Results of those transformations are then sent to the output layer, where they are weighted, summed, and again transformed to produce a prediction of the dependent variable(s). The prediction is then compared to the actual value of the dependent variable and a root mean square error is calculated. The root mean square error is then back-propagated through the network and used to adjust the weights between each layer (Smith 1996). This process, called "model training", is repeated until the root mean square error is minimized or until it has reached an arbitrary cut-off point.

For each nest in the data set, we randomly selected, without replacement, one of 10 random sampling points from within the same sampling plot and year as the nest using a random number table. Therefore, nest points were paired with random points from the same pasture, allowing us to create a balanced data set. We used QNET 2000 for WINDOWS (Vesta Services, Winnetka, Illinois) to develop neural networks. We divided the data set into training (n = 64) and test (n = 16) data sets prior to analysis. The training data set was used in model development, but the testing data set was only used to evaluate network accuracy and prevent overfitting (i.e. the mapping of the training data resulting in poor generalizability to novel data). We trained a series of networks to determine optimal number of neurons for our application. Those networks were identical except in the number of neurons in the neuron layer (range: 1–10 neurons). Each network was trained for 1,000 iterations. We selected the network with the highest correlation between observed and predicted classifications but that contained the fewest number of neurons. We measured overall accuracy of models by calculating the area under the curve for the plot of the receiver operating characteristic plot (Fielding and Bell 1997, Fielding 1999b). That measure of model accuracy is preferred to traditional measurements of accuracy (e.g. percentage correctly classified) because it is inde-

pendent of cut-off thresholds used to determine class membership (Fielding and Bell 1997, Fielding 1999b). We used the signal-detection module in SYSTAT (version 9.0, SPSS 1999) to calculate the area under the curve for the training and the test data sets using the nonparametric model option.

To determine the importance of individual variables in the network, we calculated each variable's relevance and conducted simulation analyses. Relevance is the percentage contribution (or importance) of each variable to the networks predictions (Özesmi and Özesmi 1999). Relevance of each variable is calculated as the sum of squared connection weights for the variable of interest divided by the sum of squared connection weights of all variables. Simulations were conducted by generating a data set in which the variable of interest varied incrementally between its minimum and maximum value and where most of the other variables were held constant at the overall mean (i.e. calculated from both successful and unsuccessful nests; Table 1). However, our analysis indicated that one variable was extremely important in determining network predictions (percentage structural cover; see below). To control for the effect of percentage of structural cover to determine the effects of the other variables, it was held constant at its nest-site mean. In doing so, it was assumed that the nest-site mean represented an acceptable, more optimal level for that variable with regard to nest-site selection. To contrast those simulations and demonstrate the level of importance that percentage of structural cover had, we created data sets in which percentage of structural cover was held at the mean for random points. Each simulation data set was then presented to the trained network to obtain predictions. We assumed an arbitrary cut-off threshold of 0.5 to demarcate random ($\leq$0.5) from nest (>0.5) locations. Although that results in some loss of information (Fielding and Bell 1997, Fielding 1999b), it makes graphical interpretation of the results easier. Using a cutoff equidistant from both classification extremes also allowed us to identify transition points to indicate when a point became unsuitable for a nest point or vice versa.

We used bootstrap analysis to determine the relationship between habitat variables and nest success. We used SYSTAT (version 9.0, SPSS 1999) for generating distributions of means for habitat features at successful and at unsuccessful nests. We generated 1,000 bootstrap means for each variable and used 95% confidence intervals to test for significance (Mooney and Duval 1993).

Results

Nests were not distributed equally among grazing treatments. Of the 40 nests we located in 1999 (n = 6) and 2000 (n = 34), two (5%) were located in the control pasture, 22 (55%) in moderately grazed pastures, and 16 (40%) in heavily grazed pastures. There was no apparent seasonal pattern in nest success. Among successful nests, none were found in the control pasture, six (60%) in moderately grazed pastures, and four (40%) in heavily grazed pastures. Among unsuccessful nests, two (7.1%) were located in the control pasture, 15 (53.6%) in moderately grazed pastures, and 11 (39.3%) in heavily grazed pastures. Nest densities were 0.13 nest ha^{-1} on control pastures, 0.44 nests ha^{-1} on moderately grazed pastures, and 0.37 nests ha^{-1} on heavily grazed pastures.

The neural model correctly classified 81% of nest locations in the training data. The area under the curve was 0.91 and 0.77 for training and testing data, respectively. Those area under the curve values indicate that a randomly selected nest-site case from the training data would receive a higher neural classification score than a randomly selected random point 91% of the time. Likewise, a randomly selected nest-site case from test data would receive a higher neural classification score than a randomly selected random point 77% of the time. Of variables included in the neural model, percentage of structural cover had the highest relevance score (Table 1) indicating it was the most important variable influencing nest-site selection. Structural cover (percentage), distance to nearest structural element, bare-ground exposure, and percentage of litter cover had a collective relevance of 64.6% (Table 1). Remaining variables contributed to network predictions, but each had relevance scores <10%. Therefore, results are presented only for the four most important variables as indicated by relevance scores.

Under the assumption of near-optimal structural cover, neural classification scores declined with increasing distance to structural elements. When the distance to structural elements was >270 cm, locations became unsuitable for Lark Sparrow nests (Fig. 1A). Neural classification scores also declined with increasing bare-ground exposure, and points with >87% bare ground were unsuitable (Fig. 1B). A similar pattern emerged for percentage of litter cover, indicating that plots with litter cover >74% were unsuitable (Fig. 1C). Neural classification scores increased with increasing structural cover (Fig. 1D) indicating plots with <9% structural cover were unsuitable.

Distributions of bootstrapped means for

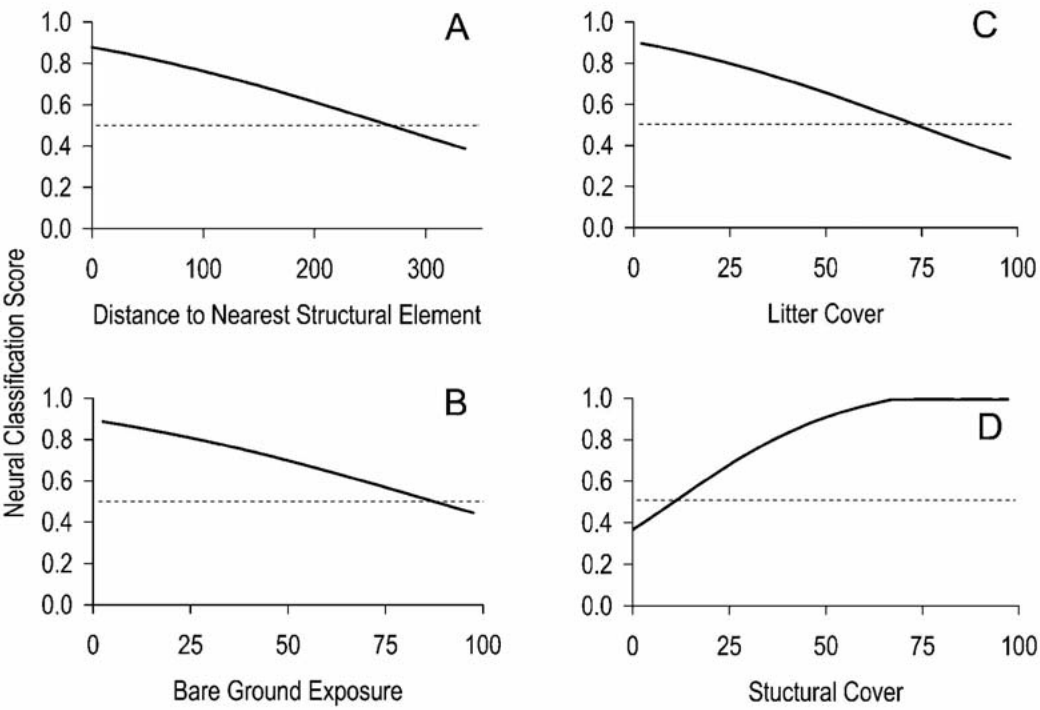

FIG. 1. Results of simulations using the trained neural network model for discriminating between Lark Sparrow nest sites and random points. Results are presented for variables with relevance scores ≥10% (Table 1): (A) distance to nearest structural element (centimeters), (B) bare-ground exposure (percentage), (C) litter cover (percentage), and (D) structural cover (percentage). Dashed horizontal lines indicate the arbitrary 0.5 cutoffs between nest and random sites.

TABLE 1. Relevance scores, overall (n = 80) and nest-site (n = 40) means (SE) for variables used in the neural-network analysis of Lark Sparrow nesting ecology in western Oklahoma, 1999–2000.

Variable	Relevance (%)	Overall mean[a]	Nest-site mean[b]
Distance to visual obstruction (m)	4.7	6.0 (0.57)	5.0 (0.77)
Litter depth (mm)	3.7	2.8 (0.41)	2.8 (0.38)
Height of tallest plant (cm)	8.8	34.2 (1.63)	37.4 (2.04)
Screening cover class	5.9	2.9 (0.16)	3.0 (0.15)
Distance to nearest structural element (cm)	12.1	31.7 (6.66)	8.0 (3.66)
Bare-ground exposure (%)	12.7	30.6 (3.78)	16.0 (3.32)
Litter cover (%)	13.6	15.3 (2.10)	11.6 (1.68)
Grass cover (%)	3.6	10.0 (1.24)	9.6 (1.82)
Forb cover (%)	8.8	10.3 (1.41)	9.1 (1.52)
Structural cover (%)	26.3	22.5 (3.23)	41.6 (4.71)

[a] Mean calculated for nest and random points.
[b] Mean calculated only for nest points.

successful and unsuccessful nests overlapped for three of the four variables that were important in the neural model. Distribution of bootstrap means overlapped for distance to the nearest structural element (Fig. 2A). Distribution of bootstrap means for structural cover also overlapped (Fig. 3B), but the range of means for structural cover at successful nests (18.05–57.05%) was twice as large as the range for unsuccessful nests (35.08–55.17%). That is, there was more variation in structural cover among successful than among unsuccessful nests. Successful nests were associated with less bare-ground exposure than unsuccessful nests (Fig. 3A). On average, successful nests had three times less bare-ground exposure than unsuccessful nests. Successful nests had nearly twice as much litter cover compared to unsuccessful nests (Fig. 2B).

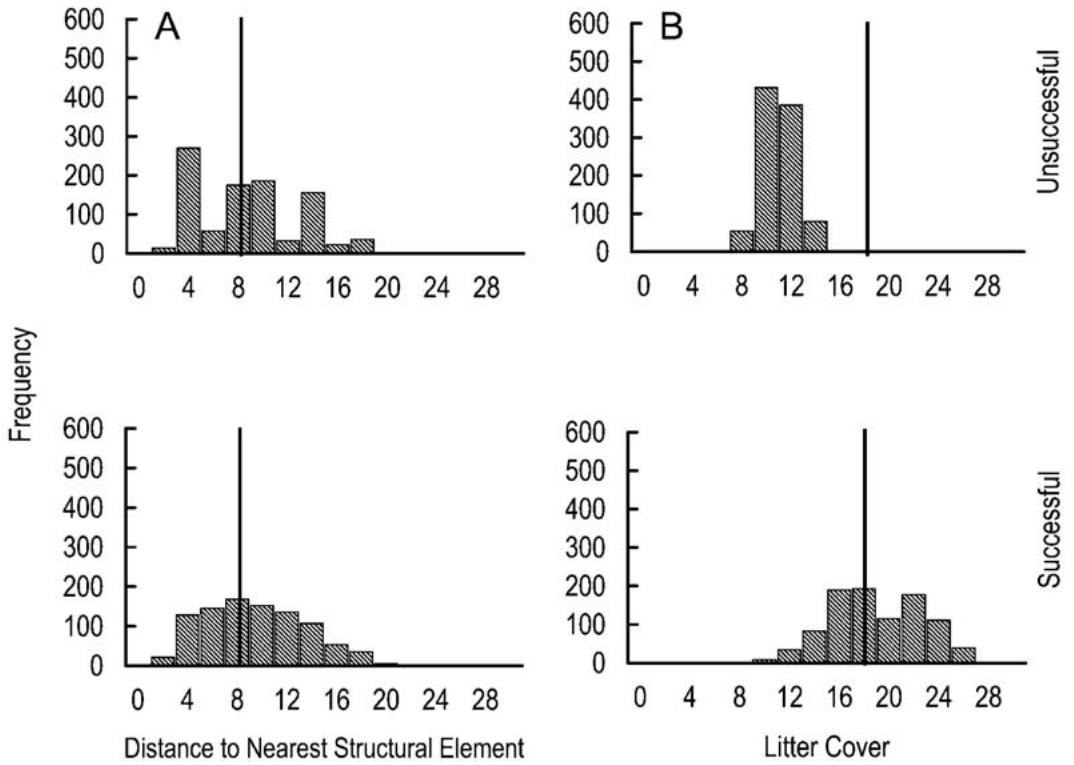

FIG. 2. Frequency diagrams of bootstrapped means for variables with relevance scores ≥10% (Table 1). Diagrams represent distribution of bootstrapped means for successful (lower row) and unsuccessful (upper row) Lark Sparrow nests for (A) the distance to nearest structural element (centimeters) and (B) litter cover (percentage). The 95% CI for successful and unsuccessful nests overlapped for (A) and (B). Vertical lines represent the mean of bootstrapped means for successful nests.

DISCUSSION

Lark Sparrows at our study site more often chose nest sites in grazed pastures, which is consistent with previous work. Bock and Webb (1984) and Bock et al. (1984) found that Lark Sparrows preferred to use grazed sites in Arizona. At those sites, Lark Sparrows were most commonly observed in short grasses (<15 cm) and on bare ground (Bock and Webb 1984).

Our finding that the amount and distribution of structural elements are important determinants of Lark Sparrows nest-site selection is also consistent with previous work. In southern Oklahoma, Newman (1970) reported that 7 of the 10 ground nests he studied were located at the base of small woody plants. Nest placement near structural cover may be an adaptation to reduce nest predation by a specific suite of predators. Martin (1993) offered two hypotheses regarding effects of vegetation on the risk of nest predation. The first hypothesis was the total-foliage hypothesis, which states that the risk of nest predation decreases as the total amount of vegetation increases (Martin 1993). That would occur due to increased difficulty of locating nests as the number of potential substrates increased. The second hypothesis is the potential-prey hypothesis, which states that the risk of nest predation decreases with increasing density of the particular nesting substrate (Martin 1993). Nests placed in locally abundant vegetation may prevent predators from forming an efficient search image, but only at low nest densities. The potential-prey hypothesis would only hold if ground nests in that particular vegetation type were relatively rare in the landscape (Schmidt and Whelan 1998). Our results tended to support the potential-prey hypothesis. The majority of Lark Sparrow nests were associated with broom snakeweed, which was abundant within the grazed pastures on

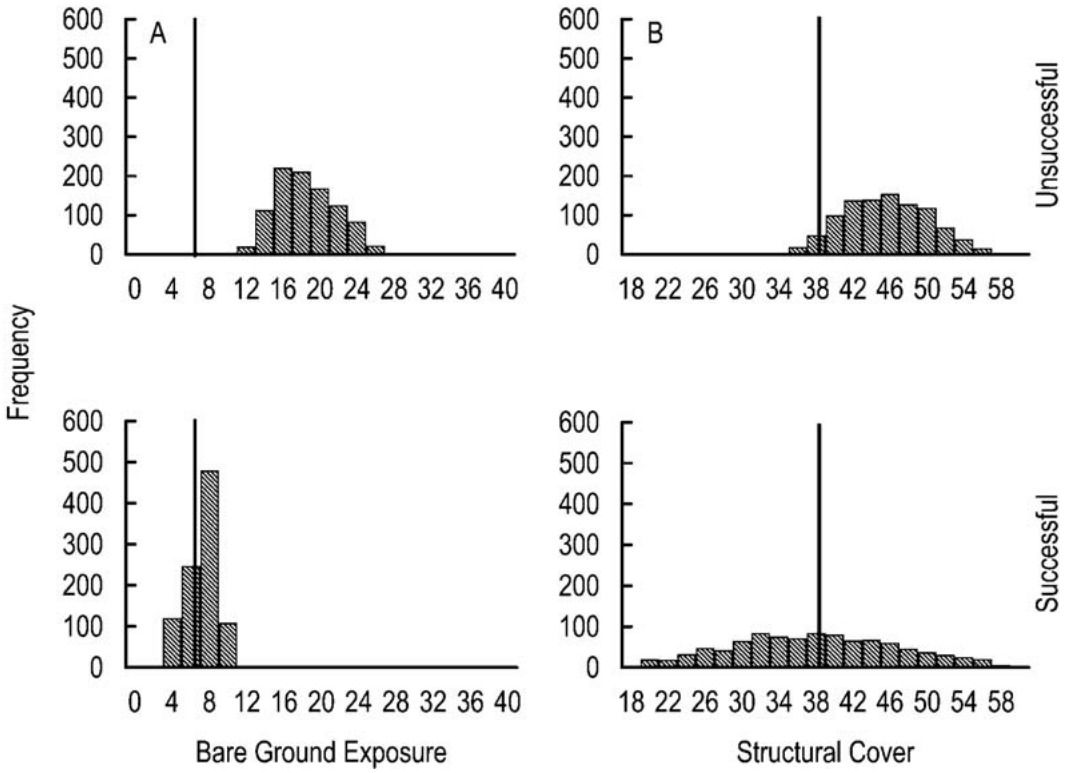

FIG. 3. Frequency diagrams of bootstrapped means for variables with relevance scores ≥10% (Table 1). Diagrams represent distribution of bootstrapped means for successful (lower row) and unsuccessful (upper row) Lark Sparrow nests for (A) bare-ground exposure (percentage), and (B) structural cover (percentage). The 95% CI for successful and unsuccessful nests overlapped for (B). Vertical lines represent the mean of bootstrapped means for successful nests.

our study site (Suedkamp 2000). However, we were not able to ascertain if nest placement in association with broom snakeweed was related to predator swamping, as predicted by the potential-prey hypothesis.

Alternatively, nest placement may be more related to issues of nest microclimate (i.e. thermal refuge hypothesis) than nest predation. Incubating eggs require a specific environment for optimal development (Walsberg 1985). Structural cover may provide nests with thermal cover, allowing them to maintain nest temperatures that are lower than the surrounding environment, or it may moderate microclimate fluctuations providing a more stable thermal environment for developing embryos. Selection for thermally tolerable nest sites has been noted for this species and others. Lark Bunting (*Calamospiza melanocorys*) nests were shaded from ambient sunlight for 60% of the day and for 40% of the midday hours, when ambient solar radiation was most intense (With and Webb 1993). Nests of Vesper Sparrows (*Pooecetes gramineus*) and Horned Larks (*Eremophila alpestris*) placed northeast of vegetation clumps had lower nest temperatures than nests placed with vegetation at other orientations (Nelson and Martin 1999). Maximum temperatures at Lark Sparrow nests were also significantly lower than at random points in western Oklahoma (Suedkamp 2000).

The potential-prey and thermal-refuge hypotheses may not be mutually exclusive. It is possible that both predation and thermal considerations have guided the evolution of nest-site selection. Characteristics of the nest site that provide protection from nest predation may also garner thermal benefits and vice versa. However, because most nests in our sample were depredated and because nest temperatures were lower than those at random locations, the thermal-refuge hypothesis seems

the best supported at this time. Therefore, it is likely that sites with close proximity to structural elements and high levels of structural cover are selected for their effects on the nest microclimate. Further research seems warranted to clarify that issue.

There was more variation in the amount of structural cover at successful nests than there was at unsuccessful nests (Fig. 3B). At first that result may seem counterintuitive, because if structural cover was an important determinant of nest-site selection, then it would be expected that successful nests would be located within a range of cover amounts, which maximizes the probability of nest success. However, different types of predators (e.g. raptors, mammals, snakes) use different foraging methods for which different amounts of structural cover provide sufficient protection (Liebezeit and George 2002). As a result, no single amount of structural cover will provide protection against all predator types, preventing optimal nest-site selection (Filliater et al. 1994, Liebezeit and George 2002). It is possible that unsuccessful nests had levels of structural cover that left them susceptible to predation by a certain predator type, resulting in a large number of nests depredated at that level of structural cover. The successful strategy in this case would be to select nest sites over a wider range of structural cover to protect nests from most of the types of predators in the area. Liebezeit and George (2002) were able to identify predators of Dusky Flycatchers (*Empidonax oberholseri*) nests with surveillance cameras and found that nests depredated by mammals were further from shrub edge, surrounded by more saplings, located in larger shrub patches, and were more concealed than nests depredated by birds. Because we were unable to identify nest predators in our study, we cannot conclusively determine if similar differences exist between site characteristics at successful and unsuccessful nests.

The comparison of habitat characteristics at successful and unsuccessful nests revealed a pattern counter to those obtained from the neural simulations for one of the four most important variables. Although simulations showed that suitability decreased as litter cover increased, bootstrap analysis showed that successful nests had more litter cover than unsuccessful nests (Fig. 2B). Nest-site selection by Lark Sparrows might be suboptimal because habitat conditions change too frequently for natural selection to refine site-selection behavior. For instance, With (1994) reported that McCown's Longspurs (*Calcarius mccownii*) preferentially nest under shrubs in some habitats, but that predation rates were also high due to predators that preferentially foraged at the same sites. However, in our study, fewer Lark Sparrow nests were placed in heavily grazed as compared to moderately grazed pastures, but the proportion of depredated nests was similar. Therefore, temporal variation in grassland communities during the lifespan of a Lark Sparrow might preclude the development of nest-placement strategies (With 1994). Studies of long-term vegetation dynamics of grazed lands indicated changes in species composition and structure vary widely through time (Smeins and Merrill 1988, Fuhlendorf et al. 2001). Despite that variation, natural selection should converge on the long-term mean conditions for nest-site selection in Lark Sparrows. An alternative hypothesis also exists. Misenhelter and Rotenberry (2000) reported a selectivity for habitat types in which fitness was less than in nonpreferred habitats for the Sage Sparrow (*Amphispiza belli*) in coastal sage scrub in southern California. Those authors suggested that the suboptimal choice of nesting habitat by this species was due to human-induced changes in landscape configuration that decoupled habitat selection from its suitability through changes in habitat use by nest predators. Livestock grazing may be one such example of human-induced change that decouples those patterns through modification of the vegetation community.

Our results suggest that management for the Lark Sparrow in the mixed-grass prairie should attempt to provide moderate levels of litter accumulation and bare-ground exposure (Fig. 1B and C). Management should also focus on creating habitat structure. Structural cover should increase the attractiveness and should decrease the distance between nests and structural elements within a habitat patch for nesting Lark Sparrows. Maintaining bare-ground exposure below 12% should also increase nest success (Fig. 3A). Although important for nest-site selection, distance to the nearest structural element (Fig. 2A) and structural cover (Fig. 3B) did not appear to influence nest success within the ranges used by Lark Sparrows at this study site.

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