

**EFFECTS OF TEMPERATURE ON NEST SITE
SELECTION OF GROUND-NESTING
GRASSLAND BIRDS**

By

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Thesis Approved:



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INTRODUCTION

Agricultural practices have affected Neotropical migratory birds in the United States more than any other land use practice (Rodenhouse et al. 1995). Grassland loss in the United States from 1982 to 2000, generated from 2 artificial neural network models. Light lines were used to designate pre-growing season data (May) and bold lines were used to designate post-growing season data (Aug). Ground temperature was shown as a function of time of day (hours) (a), wind speed (m/s) (b), light intensity (lux) (c), soil moisture (%) (d), distance to visual obstruction (m) (e), screening cover class in the fourth stratum (30-40 cm) (f), litter depth (mm) (g), bare ground (%) (h), litter cover (%) (i), grass cover (%) (j), forb cover (%) (k), and shrub cover (%) (l)..... 34

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INTRODUCTION

Agricultural practices have affected Neotropical migratory birds in the United States more than any other land use practice (Rodenhouse et al. 1995). Grassland birds in particular have declined more rapidly than any other guild of North American birds over the last 30 years (Knopf 1994). Recent declines have been most notable in the southern Great Plains states such as Oklahoma (55%), Texas (45%), and Kansas (45%) (Johnsgard 1979, Sauer et al. 1997, Hull Sieg et al. 1999). Proximate causes implicated in the decline include intensified agricultural practices, overgrazing, urban development, increasing human population pressure, climate change, and global desertification (Samson and Knopf 1994, Manning 1995). However, recent studies have suggested that increasing temperatures may play a role in these declines by decreasing the length of laying season (Klimstra and Roseberry 1975), initiating breeding earlier (Meijer et al. 1999), decreasing hatchability (Yeatter 1950, Wilson et al. 1979), altering amounts of thermally tolerable habitat space (Forrester et al. 1998), affecting microclimate selection (Wolf and Walsberg 1996), modifying temperature extremes at nests (Ricklefs and Hainsworth 1969), and constraining activity budgets (Goldstein 1984).

Predicted global climate change may exacerbate temperature fluctuations. Current studies indicate that a doubling of atmospheric carbon dioxide concentrations will be accompanied by a 1.5 – 4.5°C increase in average global surface temperatures over the next century (Verstraete and Schwartz 1991, Schneider 1993). These predictions may have dire consequences in the southern Great Plains where interior conditions may become drier as summer precipitation and soil moisture are reduced. In southern states such as Oklahoma where the majority of semi-arid land (60.1%) is rangeland (Knopf 1994), large-scale climate variations may limit avian production (Wiens 1974). Although unusually wet or dry years (deviate $\geq 25\%$ from mean) occur less than

once every 2.5 years in mixed-grass prairies (Wiens 1974), recent modeling suggests that some grassland birds are more sensitive to the magnitude of weather changes from long-term means than to interannual variation in weather variables (Lusk et al. In Press).

Agricultural practices, such as livestock grazing, are a dominant land use in the southern Great Plains (Coupland 1992, Knopf 1994), and may also negatively affect ground-nesting grassland birds. In mixed-grass prairies, heavy grazing may directly influence the amount and kind of habitat available for grassland species. Grazing might affect usable space by influencing the amount and type of cover (i.e., roosting, brooding) present on a landscape. For species such as the northern bobwhite (*Colinus virginianus*) that require a minimum of 2 habitat types (Guthery 1997), interspersion of cover and patch configuration (Guthery 1999) may be critical determinants of usable space. Grazing may further reduce the amount of usable space by causing fluctuations in the thermal environment that make some portions of grassland habitat thermally intolerable in space or time.

Specifically, grazing alters the structure and composition of vegetation in grassland communities and may subsequently modify the environment for ground-nesting birds. In prairies, grazing has been shown to alter species diversity (Coppock et al. 1983, Collins and Barber 1985, Milchunas and Lauenroth 1993), the proportion of mid grasses (Fuhlendorf and Smeins 1997, 1998), annual net primary production (ANPP), root biomass (Sims et al. 1978, Milchunas and Lauenroth 1993), litter biomass, root:shoot (Sims et al. 1978), and standing crop (Sims et al. 1978, Gillen et al. 2000). However, Milchunas and Lauenroth (1993) showed that effects of grazing were dependent on ANPP (highly correlated with precipitation), the evolutionary history of grazing on a site, and the level of consumption. The combination of these alterations in plant communities as a result of grazing, may alter spatial heterogeneity, which may ultimately increase nest depredation rates (Bowman and Harris 1980).

Grazing directly modifies the thermal environment at the nest by reducing the height of the plant canopy, which may allow more solar radiation to penetrate the vegetation (Coupland 1992). Reduced canopy height leads to increased wind penetration, which produces more rapid mixing of the air and heat dissipation (Campbell and Norman 1998). The combination of these factors may produce a more extreme thermal environment at the nest, which may limit the amount of usable space (Guthery 1997) available for ground-nesting birds. Current studies have shown that the thermal tolerance for gallinaceous grassland bird embryos ranges from 37.0 to 40.6 °C, although peak survivorship occurs at 38.6 ° (Webb 1987). Guthery et al. (2000) estimated that operative temperatures >38.7°C were sufficient to induce hyperthermia in northern bobwhites because heat gain would exceed heat dissipation. In regions such as the southern Great Plains, where peak daytime temperature may be close to or greater than thermally tolerable limits for avian species, nest microsite selection may limit activity to a greater degree than predator avoidance or food-gathering strategies (Goldstein 1984).

My goal was to evaluate the effects of grazing on the thermal environment for ground-nesting birds. Specifically, my objectives were: 1) to investigate the effects of grazing intensity on microclimate features, 2) to evaluate the effects of grazing intensity on ground temperatures, 3) to investigate the effects of thermal regimes on nest site selection for ground-nesting grassland birds, and 4) to create a model to determine which variables were the most important for predicting ground temperatures.

STUDY AREA

I conducted this research at the Marvin Klemme Experimental Range Research Station (35°25'N; 99°05'W) near Bessie, Washita County, Oklahoma. The 600-ha site is a part of the Oklahoma Agricultural Experiment Station System. Annual precipitation averages 68 cm with slightly more than two-thirds falling during the growing season

(Apr–Sep). Average summer temperatures from 1951 to 1980 were highest in July and August at 36°C. On average the first day of frost in the fall is 30 October and the last day on 8 April. The most prevalent soil is the Cordell silty clay loam (Gillen et al. 2000), which is shallow and ranges from 25 to 36 cm in depth (Moffat and Conradi 1976).

The research site is classified as southern mixed prairie and includes a variety of short and midgrasses (Coupland 1992). Typical graminoids include sideoats grama (*Bouteloua curtipendula*), blue grama (*B. gracilis*), buffalograss (*Buchloe dactyloides*), little bluestem (*Schizachyrium scoparium*), and big bluestem (*Andropogon gerardii*). Common herbaceous dicots include scurfpea (*Psoralea* sp.), Mexican sagewort (*Artemisia ludoviciana*), woolly loco (*Astragalus mollissimus*), western ragweed (*Ambrosia psilostachya*), and common broomweed (*Amphichayris dracunculoides*). Dominant woody species include smooth sumac (*Rhus glabra*), broom snakeweed (*Gutierrezia sarothrae*), and sandhill plum (*Prunus angustifolia*) (Fuhlendorf et al. In Press, Gillen et al. 2000).

There were 3 grazing treatments on the site: (1) no grazing (≥ 50 years), (2) moderate grazing, and (3) heavy grazing. In the no grazing treatment there is only one pasture that was 16 ha in size. In the moderate grazing treatment, pastures ($n = 4$) ranged from 40.8 to 57.2 ha in size and stocking rates ranged from 1.0 to 1.4 head/ha. In the heavily grazed treatment, pastures ($n = 4$) ranged from 39.5 to 46.0 ha in size and stocking rates ranged from 1.9 to 2.2 head/ha. The 2 grazing treatments supported stocker cattle for 5 consecutive months (Apr–Aug) of the year.

I randomly selected 3 pastures in each grazed treatment and the only pasture with no grazing for fixed plots. Within each grazed pasture I established 1-ha plots, hereafter called heat grids, (3 heat grids/treatment x 3 treatments = 9 heat grids). All heat grids in the no grazing treatment were located in the same pasture. Corner points of each heat grid were chosen to correspond with previously existing stakes arranged in

a 100-m grid system. Within each heat grid, I established 10 points by randomly generating x and y coordinates starting from the northwest corner (10 points/plot \times 10 plots = 90 points). I used this set of random points within each heat grid to measure temperature and vegetation variables throughout the summers of 1999 and 2000.

METHODS

Vegetation Sampling

Heat Grids (Random Points).—I sampled vegetation structure and composition in heat grids at the beginning (May) and end of the growing season (late July—early Aug). I sampled all 10 points in each heat grid for a total of 30 points per grazing treatment and 90 points per sampling period. I measured 4 structural variables, 2 measures of woody plants or homologs, and canopy cover by species at each point. I defined woody homologs as those plant species that provided structure similar to woody vegetation. These species included broom snakeweed, common broomweed, prairie acacia (*Mimosa biuncifera*), Mexican sagewort, sensitive briar (*Mimosa nuttallii*), smooth sumac, and big-top dalea (*Dalea eneandra*). Structural variables included litter depth (mm), distance to visual obstruction (m), screening cover, and emergent plant height (cm). Distance to nearest woody homolog was the primary index of shrub abundance. I measured distance to the nearest woody homolog once during the post-growing season sampling period because I assumed there would be minimal change during the summer.

I measured all of the structural variables in each cardinal direction from heat grid points with the exception of emergent vegetation height, which I measured to the north of the point. Litter depth (mm) was recorded within 0.2 m of each heat grid point. I defined distance to visual obstruction (m) as the point at which a 15-cm black marking, resembling the average height of a grassland bird, was obscured from a kneeling observer using a Robel pole (Robel et al. 1970). I measured screening cover by estimating cover classes within each horizontal 0.1-m stratum using a density board

(Nudds 1977). Finally, I measured the distance to the nearest woody homolog in each quadrant. I measured the remaining structural and compositional variables using a Daubenmire frame (Daubenmire 1959) placed immediately north of each heat grid point. I defined emergent vegetation height (cm) as the tallest plant in the Daubenmire frame. I also recorded canopy cover by species and the percent rock, bare ground, and litter cover within the frame.

Nests.--At the end of breeding season after nests were inactive, I measured all the previously mentioned variables with some modifications and additions. I sampled vegetation once at the end of the breeding season concordant with the end of the growing season. All structural variables were measured in the same manner but emergent vegetation height and canopy cover by species were measured by centering the Daubenmire frame on the nest as opposed to placing it to the north. In addition, I measured nest substrate (bare ground, litter, plant species) and orientation of nest entrance (degrees) if appropriate. I did not measure orientation for species that build cup nests and enter from above such as lark sparrows (*Chondestes grammacus*).

Thermal Environment Sampling

Heat Grids.--I measured 6 thermal variables to the north of each heat grid point monthly from May to August during the summers of 1999 and 2000. I sampled heat grids at random in blocks of 3 (1 from each treatment) to minimize the confounding effect of time on temperature. Each block of 3 heat grids was sampled on the same day to minimize daily variation in temperature. I confined sampling to consecutive days each month between 1100 and 1700 hours. I sampled during this period to capture peak daily temperatures. The 3 temperature variables ($^{\circ}\text{C}$) were ground temperature, temperature at bird level (15 cm), and temperature at 1 m. I sampled at 1 m because the majority of vegetation was <1 m and should not influence temperature at this height. I also measured wind speed (m/s), light intensity (lux), and soil moisture (%) at each point.

During each monthly sampling period I measured temperature continuously at 3 randomly selected points per treatment using HOBO dataloggers (Onset Computer Corporation, Pocasset, Massachusetts, USA). I was programmed to start recording at the

All 3 temperature measurements and wind speed were taken using a portable thermometer accurate to 0.1°C and anemometer (Omega Engineering, Stamford, Connecticut, USA). I recorded temperature as the 3-s average given after temperature peaked north of the point. I then recorded the highest wind speed over a 1-minute period. I measured light intensity using a portable light meter accurate to 1.0 lux (Extech Instruments, Waltham, Massachusetts, USA) after light intensity stopped increasing. If lux measurements were fluctuating due to changing cloud cover or wind, I waited 5 s and resampled light intensity. I calculated soil moisture gravimetrically by collecting the top 10 cm of soil with an auger and drying at 105°C for ≥ 2 days. I weighed all wet soils within 6 hours of collection to 0.1 g using a portable scale in the field, and then sealed them with electrical tape for transport back to the laboratory. I weighed all dry soils immediately after cooling on the same scale.

Nests.--I did not measure all thermal variables at nests monthly to avoid possible negative influences on bird activity. Measuring all thermal variables at a heat grid point took 1–5 minutes per sampling period per month so I did not measure all thermal variables. To minimize potential adverse effects, I measured temperature continuously at a subsample of nests each month using dataloggers. Each month I randomly divided 8 dataloggers among nests in each grazing treatment to measure temperature intensity (max temperature) and duration (length of critical temperatures). I defined critical temperature as those that exceeded 39°C. I used this temperature as a benchmark because it approximated the point at which heat gain exceeds heat dissipation, concordant with reported upper thermal tolerance limits for optimal survival in embryo

and adult birds (Webb 1987, Guthery et al. 2000): Due to an uneven number of dataloggers per treatment, I randomized the treatment receiving fewer dataloggers ($n = 2$) among months within a year. Dataloggers were programmed to start recording at the beginning of each monthly sampling period (1100 hours) and terminated within 2 hours of collection at the end of the sampling period the following day (1700 hours). With the help of a field assistant, I programmed all dataloggers to record temperature in 5-s intervals throughout each monthly sampling period.

Nest Searching and Monitoring

I searched for nests from May through early July during the breeding seasons of 1999 and 2000 by using systematic searches combined with walking haphazard paths through pastures. Nest searching among treatments and pastures was randomized to equalize observer search time among grazing treatments. After locating a nest, I marked it with a rock pile and fluorescent flagging ≥ 5 m away in 2 directions. I recorded the date, species, nest stage, contents, parental activity, and presence of any non-host eggs. Nests were monitored every 3–4 days, but nest success and daily survival rate data will not be presented here. I monitored all nests 3 times after fledging, abandonment, or depredation to determine a final fate. Any nests that I did not record activity at for 3 successive visits were then sampled for vegetation measurements described previously.

Data Analysis

I used SYSTAT version 9.0 (SPSS 1996) for all analyses listed below. I also used Excel version 97.02 (Microsoft 1997) to generate scatter plots with smoothed lines for displaying the distribution of bootstrap means at random and nest points in Figs. 2–3, and the simulation data in Figs. 4A–L. I used 95% confidence intervals to test for effects using a significance level of $P < 0.05$. In these tests, I assumed the results of the null hypotheses were known (i.e. grazing has no effect). Therefore, I focused on the

magnitude of effect instead of providing redundant *P* values throughout the text (Cherry 1998, Johnson 1999).

Microclimate Features.—I performed a factor analysis on the correlation matrix for all structural vegetation variables measured in heat grids to reduce the data set and eliminate problems of multicollinearity (Johnson 1980). For analysis of microclimate features, I combined cover data from individual categories species into broad categories according to Diggs et al. (1999). Microclimate features were then grouped into the following categories: percent rock, bare ground, litter, grass, forb, and shrub. To test for effects of grazing treatment (no grazing, moderately, or heavily grazed), sampling time (pre or post growing season), and year (1999 or 2000), I constructed 95% confidence intervals around means using the Bonferroni correction to adjust for multiple comparisons (Sokal and Rohlf 1995). Nest vegetation data were analyzed similarly testing for the effects of grazing treatment (no grazing, moderately, or heavily grazed) and year (1999,2000) within each bird species ($n = 5$). I included those species with > 9 nests over the 2-year study period. In Fig. 1, I used asterisks (*) to indicate that confidence intervals between nest and random point microclimate features did not overlap.

Thermal Environment Sampling.—I also performed a factor analysis on the thermal variables to reduce the data set and eliminate multicollinearity (Johnson 1998). To test for effects of grazing treatment (no grazing, moderately, and heavily grazed), sampling month (May, Jun, Jul, and Aug), and year (1999, 2000) on thermal variables I also constructed 95% confidence intervals using the Bonferroni correction to adjust for multiple comparisons (Sokal and Rohlf 1995). In Table 3, I used asterisks (*) to show confidence intervals that did not overlap.

Avian Data.—Datalogger sample sizes were limited among treatments and by species, so I pooled across grazing treatments within sampling month. In doing so, I

assumed that avian nest site selection, as indicated by nest vegetation variables, would not vary based on grazing treatment. Throughout the remainder of this document, I will use the term selection to mean the process of choosing resources (Johnson 1980). Throughout the results and discussion section, I will avoid using subjective terms such as preference or avoidance (Hall et al. 1997), and instead emphasize differences in magnitude between bird and random points, which I will refer to as sensitivity. I tested the assumption that grazing intensity and year would not affect nest site selection by comparing 95% confidence intervals with Bonferroni corrections around mean values of each vegetation variable across treatments within bird species. Confidence intervals did overlap across treatments for all bird species, so my assumption appeared valid.

Next, I extracted the maximum temperature for each datalogger by species within a sampling month and year. I also recorded the number of times that temperature was $\geq 39^{\circ}\text{C}$ at each datalogger within a sampling month and year by species. Then, I calculated the proportion of time that exceeded this benchmark value ($P > 39^{\circ}\text{C}$) during each monthly sampling period beginning at 1100 hours on the first day and terminating at 1700 hours the following day. These 2 variables were analyzed similarly for heat grids by pooling across grazing treatments within each sampling month and year.

Due to limited datalogger sample sizes among bird species in each sampling month, and an unknown probability distribution, I used bootstrapping for each variable mean. Bootstrapping is a non-parametric, resampling procedure that provides an empirical estimate of a sampling distribution without being constrained by assumptions about the distribution *a priori* (Mooney and Duval 1993, Davison and Hinkley 1997). I generated 1,000 bootstrap means for each sampling month, year, and bird species (only dataloggers at nests, not heat grids). I sorted each set of 1,000 bootstrap means and generated frequency histograms using the scatter plot function with a smoothed line in

Excel (v9.0.2720, Microsoft Corporation, Seattle, Washington, USA). I used a smoothed line to represent the sampling distribution of bootstrapped means for both variables at random (heat grid) points in all subsequent figures. Vertical lines represent means for each bird species within a sampling month and year. Dashed vertical lines represent nests with $n = 1$.

I used 95% confidence intervals to test for differences in maximum temperature and proportion of time $> 39^{\circ}\text{C}$ between nests and random points. However, I only tested those differences that were not biologically obvious during visual inspection. In general, this meant I tested differences between nest and random points if the nest mean for a species clearly fell within the distribution of bootstrapped means. For example, in Fig. 2b I tested the difference between the common nighthawk (C) and random point bootstrap means because they were not obviously different. Conversely, in Fig. 2e I did not test the difference between the lark sparrow (L) and random point bootstrap means because they did appear obviously different (i.e. the lark sparrow mean was outside of the random point bootstrap mean distribution).

Artificial Neural Networks.—I used artificial neural networks to determine the most important predictors of ground temperature. Subsequent simulations can then be used to elucidate the relationship between ground temperature and the vegetation and thermal variables. Neural networks are adaptive models that are analogous to the learning process in human brains (Smith 1996, Abdi et al. 1999). Neural networks are often more powerful than traditional statistical techniques because they are not subject to assumptions about relationships between existing variables *a priori*, and can be used with non-linear relationships (Smith 1996). In all subsequent analyses, I used error backpropagation multiplayer perceptron models built in Qnet 2000 for Windows (v2000, Vesta Services, Winnetka, Illinois, USA).

The data set I used in the first neural network included vegetation and thermal variables from the first monthly heat grid sampling period (mid-May) and the pre-growing season vegetation-sampling period (mid to late May). I included 17 independent variables as predictors of ground temperature (response variable). Independent variables included 3 measures of vegetation structure (distance to visual obstruction, screening cover, and litter depth), 3 measures of the thermal environment (wind speed, light intensity, and soil moisture), 5 measures of composition (percent bare ground, litter, grass, forb, and shrub cover), time of day sampled, 2 years (1999, 2000), and 3 grazing treatments (no grazing, moderately, and heavily grazed). The second neural network was similar except it included data from the last monthly sampling period and post-growing season vegetation-sampling period in August 2000. As a result, the latter model contained 15 independent variables because it did not include years. I selected the 6 vegetation variables because they were uncorrelated and explained additional variation in previous factor analyses.

Prior to running each model, I randomly allocated 20% of each data set for validation and the remaining 80% for training (Lusk et al. In Press). In the first neural model, there were 35 test cases and 144 training cases. In the second model, there were 17 test cases and 72 training cases. All models were initially run for 10,000 iterations with a maximum learning rate of 0.9, and momentum of 0.8 (Smith 1996, Lusk et al. In Press). After the first training session for each model, I examined the residual mean square error to optimize the number of iterations. I choose the optimal number of neurons by selecting the number with the smallest predicted error between the training and validation data sets (Smith 1996).

The last step in the neural network model was to expose the trained model with the optimal number of neurons to simulation data and evaluate response curves. To do this, I created a separate simulation data set for each continuous variable. Each data

set allowed the variable of interest to range between extremes while holding all other variables constant at their mean (or median if categorical). By running each simulation data set through the trained model, I examined the relationships between ground temperature and each predictor value by graphing the response curves. By adjusting the scale on each graph to the same range of ground temperatures, I was able to determine the shape of the relationship between ground temperature and each independent variable. Relationships denoted by a straight line with no slope indicated that ground temperature was either not affected, or minimally affected by changes in the predictor variable.

RESULTS

Vegetation

Screening cover in the fourth stratum (30–40 cm aboveground) had the highest component loading within the first factor (Table 1). Screening cover in the seventh stratum (60–70 cm aboveground) had the highest component loading within the second factor for the pre-growing season, but the eighth stratum (70–80 cm aboveground) had the highest component loading for the post-growing season sampling period. Litter depth had the highest component loading within the third factor. I used factor analysis as a data reduction tool; therefore, I excluded variables from further analyses if they did not have the highest component loading within each factor with 2 exceptions. Although distance to visual obstruction was correlated with screening cover and did not have the highest component loading within factor 1, I included it in additional analyses because it was a biologically important and interpretable variable. I excluded screening cover strata 7 and 8, which had the highest component loadings in factor 2 because they were correlated with stratum 4, which was already selected for further analysis. In addition, I interpreted factor 2 to be related to lack of cover, so strata 7 and 8 were probably related

Table 1. Component loadings for vegetation structure variables at random points ($n = 90$) during the pre- (May) and post-growing season (Aug) sampling periods at the Marvin Klemme Experimental Range Research Station, Bessie, Oklahoma, 1999–2000.

Season	Variable	Component loadings		
		Factor 1	Factor 2	Factor 3
May	Litter depth (mm)	0.404	-0.406	-0.744
	Distance to visual obstruction (m)	-0.698	0.450	0.056
	Screening cover class (stratum 1) ^a	0.589	-0.449	0.080
	Screening cover class (stratum 2) ^a	0.784	-0.350	0.110
	Screening cover class (stratum 3) ^a	0.877	-0.096	0.062
	Screening cover class (stratum 4) ^a	0.881	0.232	0.019
	Screening cover class (stratum 5) ^a	0.817	0.454	0.041
	Screening cover class (stratum 6) ^a	0.748	0.589	-0.059
	Screening cover class (stratum 7) ^a	0.675	0.629	-0.097
	Screening cover class (stratum 8) ^a	0.634	0.542	-0.209
	Height of tallest plant (cm)	0.520	-0.393	0.078
Aug	Litter depth (mm)	0.469	-0.407	-0.719
	Distance to visual obstruction (m)	-0.671	0.437	-0.279
	Screening cover class (stratum 1) ^a	0.487	-0.470	0.265
	Screening cover class (stratum 2) ^a	0.768	-0.471	0.154
	Screening cover class (stratum 3) ^a	0.826	-0.359	0.073
	Screening cover class (stratum 4) ^a	0.885	-0.072	0.024
	Screening cover class (stratum 5) ^a	0.881	0.105	0.085
	Screening cover class (stratum 6) ^a	0.827	0.312	0.070
	Screening cover class (stratum 7) ^a	0.773	0.465	0.022
Screening cover class (stratum 8) ^a	0.727	0.539	-0.034	

Table 1. Continued.

Season	Variable	Component loadings		
		Factor 1	Factor 2	Factor 3
	Height of tallest plant (cm)	0.446	-0.326	-0.002
	Percent of total variance explained	51.19	17.30	6.15

^a Screening cover (%) was recorded in classes for each 10-cm stratum on a density board according to Nudds (1977).

Table 2. Mean habitat features at random points ($n = 30$ points/treatment) in 3 grazing intensities during the pre- (May) and post-growing season (Aug) at the Marvin Klemme Experimental Range Research Station, Bessie, Oklahoma, 1999–2000.

Year	Season	Variable	No Grazing		Moderate		Heavy	
			\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
1999	May	Visual obstruction (m)*	5.8	0.6	8.2	0.8	9.9	0.8
		Litter depth (mm)*	9.0	1.9	7.0	1.8	3.0	0.6
		Screening cover class ^b	1.0	0.3	1.0	0.2	1.0	0.2
		Bare ground (%)	27.9	5.8	31.9	5.8	47.6	6.7
		Litter cover (%)	41.6	5.6	29.3	5.1	25.1	4.1
		Grass cover (%)	10.1	2.5	9.5	1.5	16.8	2.6
		Forb cover (%)	19.8	3.0	16.6	2.4	17.2	1.8
		Shrub cover (%)	2.8	1.4	3.3	1.4	1.5	0.7
1999	Aug	Nearest woody homolog (cm) ^a	114.0	77.0	56.0	21.3	24.0	3.3
		Visual obstruction (m)	7.4	0.8	10.1	0.7	9.7	1.0
		Litter depth (mm)*	10.0	1.6	6.0	1.1	3.1	0.8
		Screening cover class ^b	2.0	0.3	1.0	0.2	1.0	0.3
		Bare ground (%)*	10.5	2.2	17.7	3.6	37.0	5.8
		Litter cover (%)	23.4	3.7	26.4	4.4	13.0	2.1
		Grass cover (%)	6.6	1.0	9.7	1.8	13.8	2.1
		Forb cover (%)	17.0	2.3	20.5	2.7	14.2	1.9
		Shrub cover (%)	4.2	1.1	5.3	1.8	2.6	1.3
2000	May	Visual obstruction (m)*	5.2	0.6	11.7	1.0	10.4	1.2

Table 2. Continued.

Year	Season	Variable	No Grazing		Moderate		Heavy	
			\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
		Litter depth (mm)*	7.0	1.1	3.0	0.5	2.0	0.5
		Screening cover class ^b	2.0	0.3	1.0	0.1	1.0	0.3
		Bare ground (%)	24.0	5.3	40.8	5.8	47.9	6.4
		Litter cover (%)	27.5	3.5	19.6	3.3	12.9	2.8
		Grass cover (%)	14.1	2.9	15.3	2.9	14.3	2.9
		Forb cover (%)	18.8	3.2	21.4	3.0	14.9	3.0
		Shrub cover (%)	4.1	1.5	7.2	2.2	4.0	1.5
2000	Aug	Nearest woody homolog (cm) ^a	117.0	32.1	306.0	92.1	90.0	22.6
		Visual obstruction (m)	3.4	0.6	5.3	0.7	5.4	1.0
		Litter depth (mm)	6.0	1.4	3.0	0.8	2.4	0.6
		Screening cover class ^b	2.0	0.3	2.0	0.3	2.0	0.3
		Bare ground (%)	29.5	6.1	44.8	6.6	52.0	7.3
		Litter cover (%)*	38.9	6.2	20.8	5.3	15.3	3.3
		Grass cover (%)	5.8	1.5	7.9	2.4	12.2	2.7
		Forb cover (%)	12.1	2.6	10.3	2.4	11.5	2.9
		Shrub cover (%)	2.6	0.8	3.8	1.5	2.1	0.7

* 95% CI's adjusted for multiple comparisons did not overlap among treatments.

^a Distance to nearest woody homolog was not measured in the pre-growing season (May).

^b Screening cover class in stratum 4 (30 – 40 cm) was displayed because it had the highest component loading in the first factor, which explained 51.2% of the total variance.

Table 3. Mean ground temperature (°C) at random points in 3 grazing treatments ($n = 30$ /treatment) at the Marvin Klemme Experimental Range Research Station, Bessie, Oklahoma, 1999–2000.

Year	Month	No Grazing		Moderate		Heavy	
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
1999	May*	33.1	0.7	31.5	0.5	29.3	0.4
	Jun	36.5	0.7	37.1	1.1	39.5	0.6
	Jul	39.7	0.4	37.8	0.7	40.3	0.5
	Aug*	49.7	0.3	45.4	0.7	47.4	0.8
2000	May	25.2	0.6	26.0	0.6	27.1	0.3
	Jun	28.8	0.4	28.6	0.3	28.8	0.4
	Jul	42.6	1.4	39.1	0.9	42.7	1.1
	Aug	45.5	0.5	44.7	0.9	44.2	0.4

* 95% CI's adjusted for multiple comparisons did not overlap among treatments.

Table 4. Mean habitat features at nests of 5 ground-nesting grassland bird species in 3 grazing intensities at the Marvin Klemme Experimental Research Range, Bessie, Oklahoma, 1999--2000.

Species	Variable	No Grazing			Moderate			Heavy		
		<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE
Common nighthawk	Nearest woody homolog (cm)	2	27.0	5.5	7	42.0	14.6	3	15.0	4.4
	Visual obstruction (m)		12.3	3.7		12.4	0.8		16.6	4.6
	Screening cover class ^a		0.0	0.0		1.0	0.8		0.0	0.3
	Litter depth (mm)		0.0	0.0		2.0	1.8		0.0	0.2
	Bare ground (%)		62.5	0.0		63.6	13.1		70.0	7.5
	Grass cover (%)		51.3	48.8		5.7	2.1		1.7	0.8
	Forb cover (%)		20.0	0.0		17.1	6.0		4.2	2.2
	Shrub cover (%)		1.3	1.3		2.5	2.1		6.7	4.2
Grasshopper sparrow	Nearest woody homolog (cm)	1	9.0 ^b	NA ^b	11	23.0	5.3	10	348.0	205.6
	Visual obstruction (m)		9.1 ^b	NA ^b		5.4	1.4		5.4	1.6
	Screening cover class ^a		0.0 ^b	NA ^b		1.0	0.4		2.0	0.3
	Litter depth (mm)		3.0 ^b	NA ^b		6.0	1.6		5.0	1.2

Table 4. Continued.

		No Grazing			Moderate			Heavy		
		<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE
Lark sparrow	Bare ground (%)		15.0 ^b	NA ^b		17.7	6.0		8.5	3.6
	Grass cover (%)		2.5 ^b	NA ^b		19.3	8.3		25.3	5.3
	Forb cover (%)		10.0 ^b	NA ^b		14.3	3.2		5.0	1.1
	Shrub cover (%)		2.5 ^b	NA ^b		12.3	7.5		6.0	3.8
	Nearest woody homolog (cm)	2	9.0	1.5	23	5.0	2.1	23	10.0	7.2
	Visual obstruction (m)		6.7	3.6		5.1	1.1		3.9	0.8
	Screening cover class ^a		1.0	1.0		1.0	0.2		1.0	0.3
	Litter depth (mm)		8.0	1.9		4.0	0.5		2.0	0.3
	Bare ground (%)		26.3	11.3		12.5	3.1		19.1	4.9
Meadowlark s	Grass cover (%)		21.3	18.8		7.7	2.6		8.2	1.4
	Forb cover (%)		7.5	0.0		9.0	2.3		8.5	1.6
	Shrub cover (%)		8.8	6.3		51.0	6.2		38.6	5.5
	Nearest woody homolog (cm)	2	200.0	89.5	5	454.0	369.2	2	4.0	4.0
	Visual obstruction (m)		2.0	1.8		3.0	1.2		6.8	1.0

Table 4. Continued.

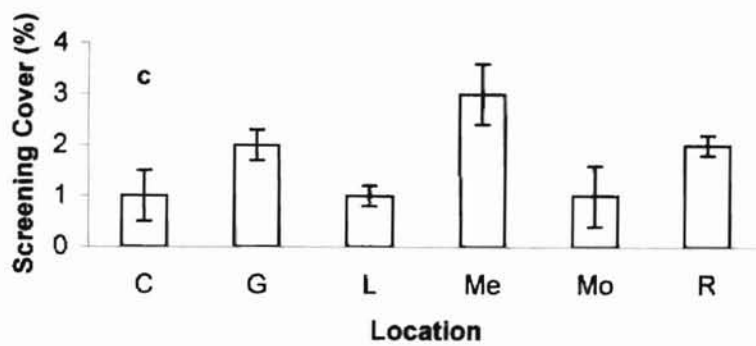
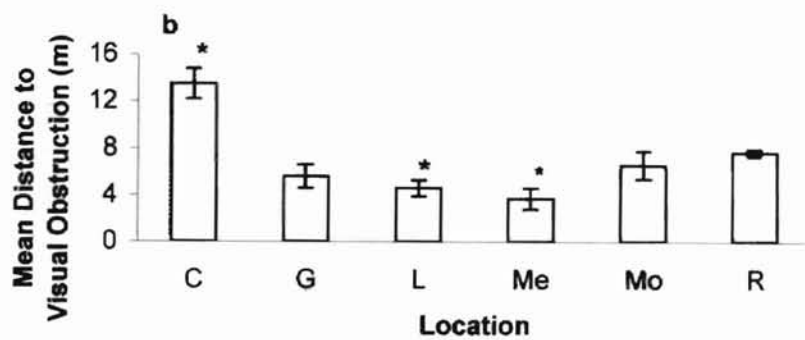
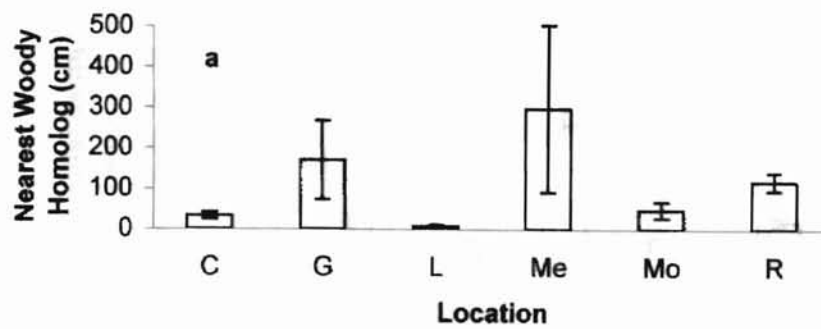
		No Grazing			Moderate			Heavy		
		<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE
	Screening cover class ^a		3.0	0.9		4.0	1.0		2.0	0.4
	Litter depth (mm)		24.0	4.1		17.0	6.4		7.0	4.5
	Bare ground (%)		2.5	0.0		2.5	0.0		8.8	6.3
	Grass cover (%)		10.0	7.5		21.0	5.7		5.0	2.5
	Forb cover (%)		11.3	6.3		12.5	6.7		12.5	5.0
	Shrub cover (%)		0.0	0.0		15.5	12.1		8.8	6.3
Mourning dove	Nearest woody homolog (cm)	5	23.0	14.5	7	51.0	41.0	4	76.0	37.3
	Visual obstruction (m)		5.0	2.2		8.4	1.8		5.6	2.2
	Screening cover class ^a		1.0	0.3		1.0	0.5		1.0	0.6
	Litter depth (mm)		5.0	0.4		3.0	0.8		1.0	0.3
	Bare ground (%)		12.0	6.8		12.9	4.7		35.6	15.7
	Grass cover (%)		5.0	2.5		5.0	1.7		9.4	4.0
	Forb cover (%)		18.0	11.3		10.7	3.1		7.5	3.4
	Shrub cover (%)		28.5	15.8		15.7	6.1		18.8	10.8

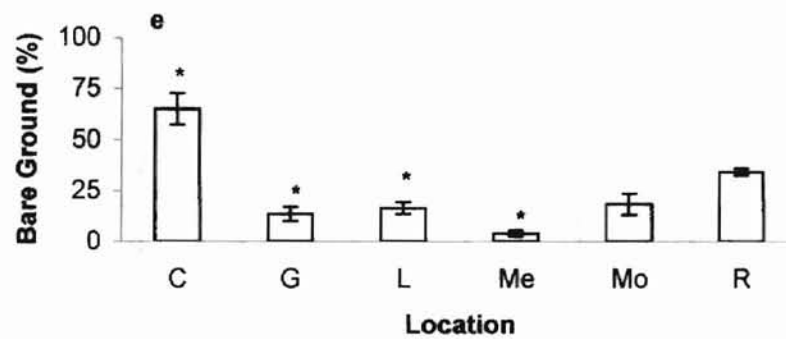
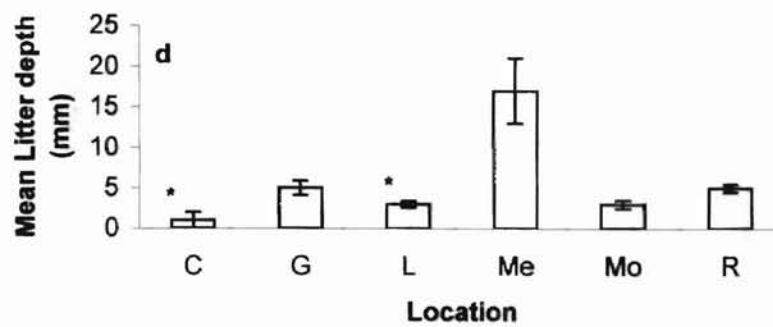
Table 4. Continued.

^a Screening cover classes from the fourth stratum (30 – 40 cm) were used because they had the highest component loading in the first factor, which explained 51.2% of the total variance.

^b Sample size was $n = 1$ in the no grazing treatment so the exact value was shown and the standard error was not applicable.

Fig. 1. Mean habitat features shown with 1 SE for random points ($n = 90$) and nests of 5 ground-nesting grassland species at the Marvin Klemme Experimental Range Research Station, Bessie, Oklahoma, 1999--2000. Asterisks (*) shown indicate confidence intervals that did not overlap between nest and random point attributes. Species codes were common nighthawk (C), grasshopper sparrow (G), lark sparrow (L), eastern and western meadowlark (Me), and mourning dove (Mo). Sample sizes were common nighthawk ($n = 12$), grasshopper sparrow ($n = 22$), lark sparrow ($n = 48$), meadowlarks ($n = 9$), and mourning dove ($n = 16$). Dependent variables shown for all species and random points were distance to the nearest woody homolog (cm) (a), distance to visual obstruction (m) (b), screening cover class in the fourth stratum (30–40 cm) (c), litter depth (mm) (d), bare ground (%) (e), litter cover (%) (f), grass cover (%) (g), forb cover (%) (h), and shrub cover (%) (i).





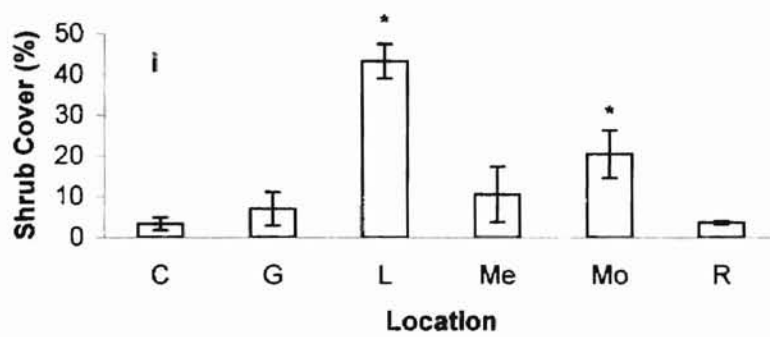
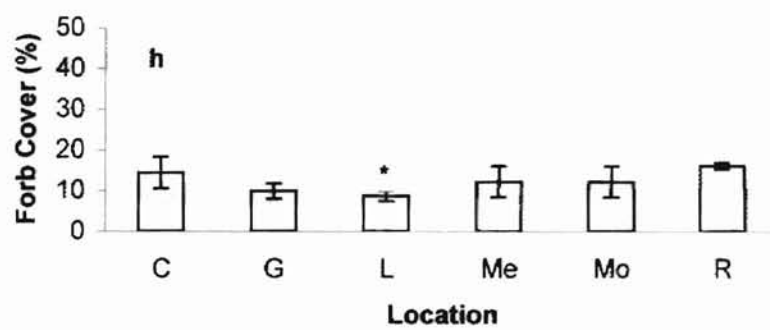
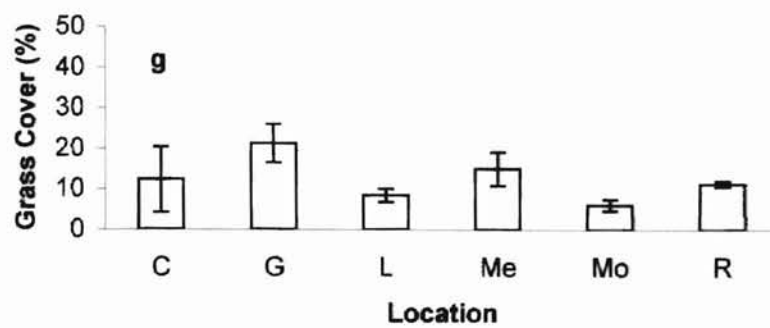


Fig. 2. Bootstrap means for maximum ground temperature ($^{\circ}\text{C}$) at random points and nests of 5 ground-nesting grassland bird species at the Marvin Klemme Experimental Range Research Station, Bessie, Oklahoma 1999–2000. Distributions of the bootstrapped means for random points were shown as a smooth curve. Mean bootstrap values for each species were shown as vertical lines. Dashed vertical lines were shown for nests with $n = 1$. Asterisks (*) were shown to indicate differences between nest and random point bootstrap means if confidence intervals did not overlap. Only comparisons that were not biologically obvious were tested. Arrows indicated the location of a species bootstrap means if not clearly visible. Species codes were common nighthawk (C), grasshopper sparrow (G), lark sparrow (L), eastern and western meadowlarks (Me), and mourning dove (Mo). Average maximum ground temperatures are shown for May 1999 (a), May 2000 (b), Jun 1999 (c), Jun 2000 (d), Jul 1999 (e), Jul 2000 (f), Aug 1999 (g), and Aug 2000 (h).

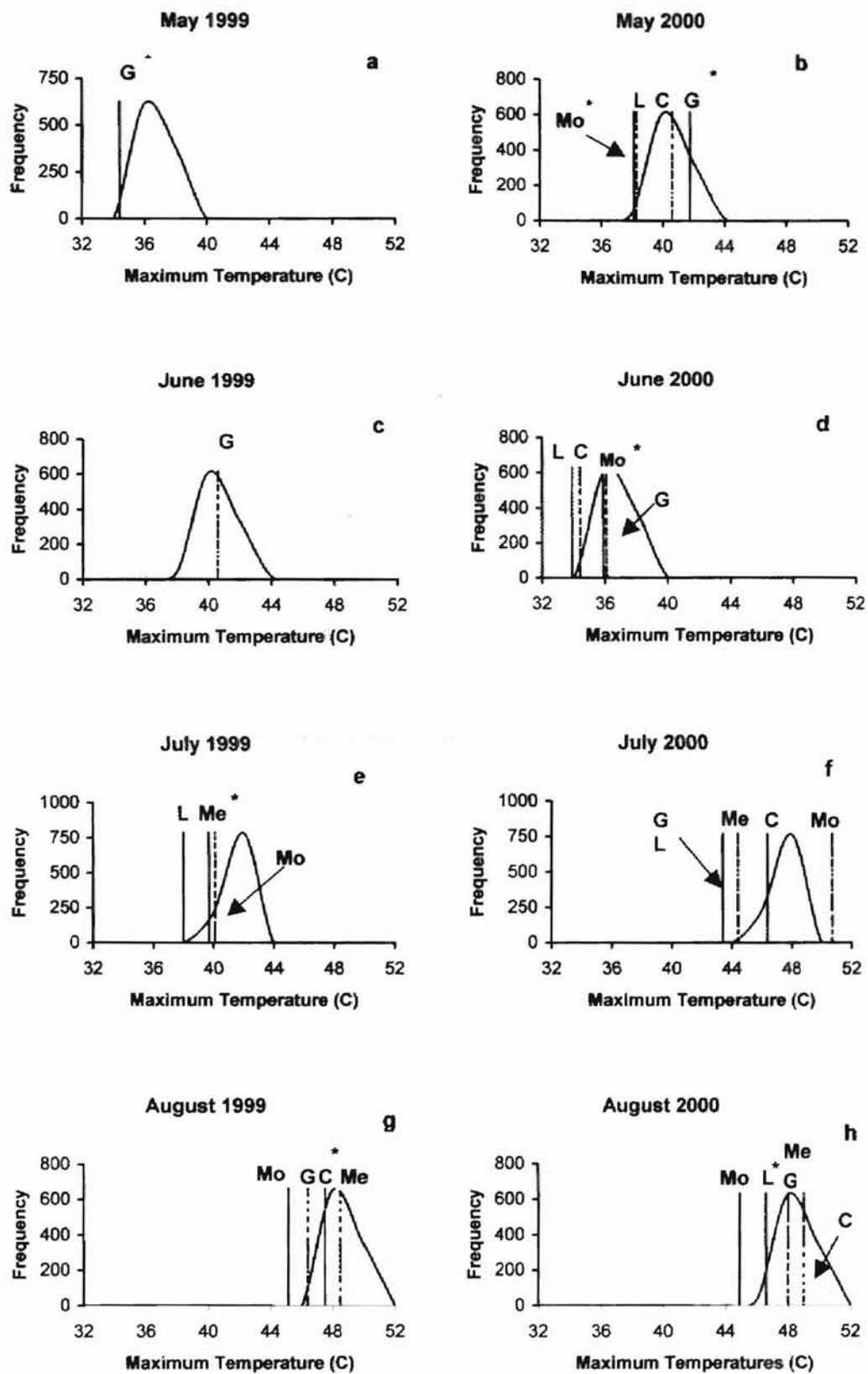


Fig. 3. Bootstrap means for proportion of time $>39^{\circ}\text{C}$ ($P >39^{\circ}\text{C}$) at random points and nests of 5 ground-nesting grassland bird species at the Marvin Klemme Experimental Range Research Station, Bessie, Oklahoma 1999–2000. Distributions of the bootstrapped means for random points were shown as a smooth curve. Mean bootstrap values for each species were shown as vertical lines. Dashed vertical lines were shown for nests with $n = 1$. Asterisks (*) were shown to indicate differences between nest and random point bootstrap means if confidence intervals did not overlap. Only comparisons that were not biologically obvious were tested. Arrows indicated the location of a species bootstrap means if not clearly visible. Species codes were common nighthawk (C), grasshopper sparrow (G), lark sparrow (L), eastern and western meadowlarks (Me), and mourning dove (Mo). Average maximum ground temperatures are shown for May 1999 (a), May 2000 (b), Jun 1999 (c), Jun 2000 (d), Jul 1999 (e), Jul 2000 (f), Aug 1999 (g), and Aug 2000 (h).

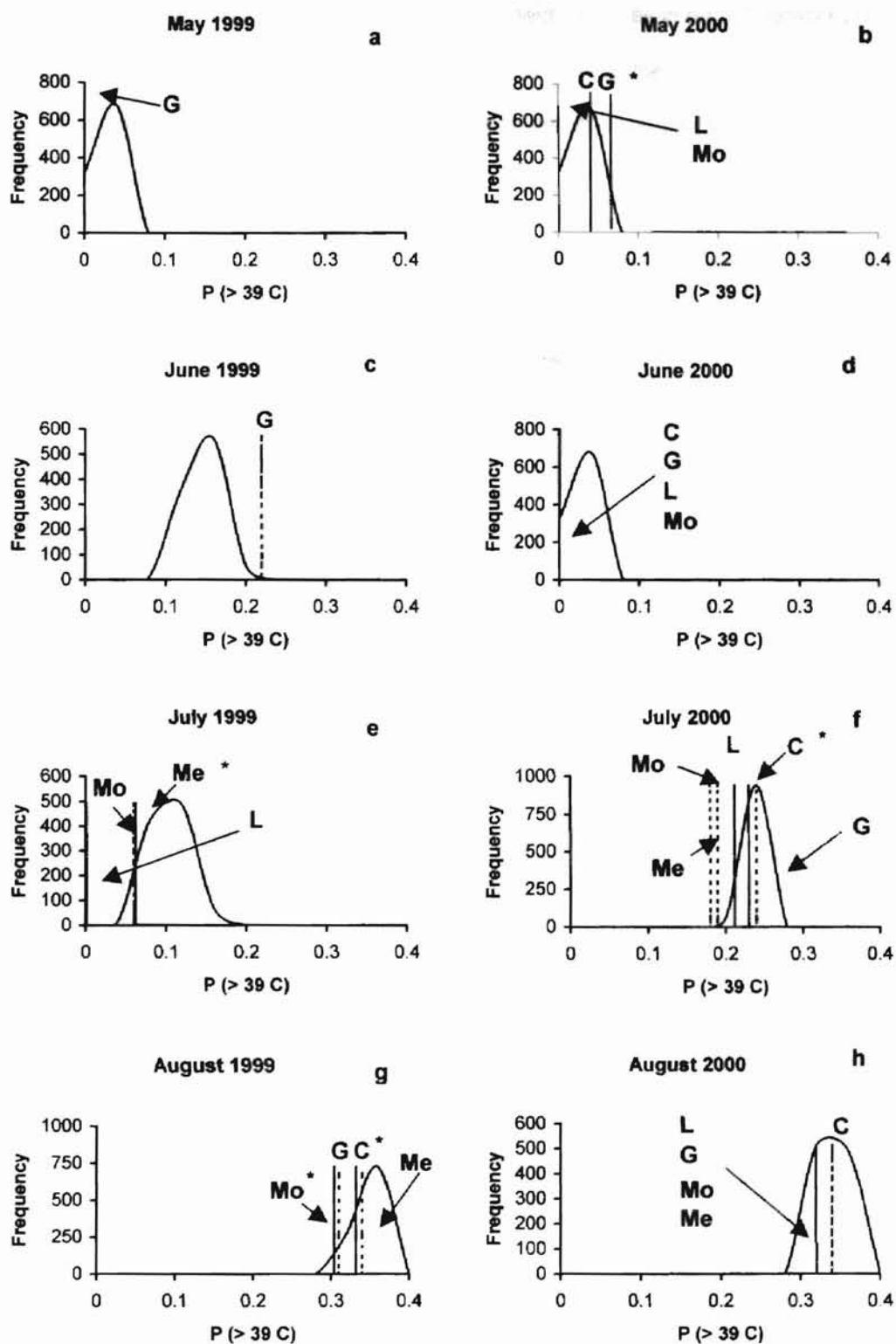


Table 5. Percent contribution values for the independent variables in neural networks models predicting ground temperature ($^{\circ}\text{C}$) at random points ($n = 90$) at the beginning (May) and end of the growing season (Aug) at the Marvin Klemme Experimental Range Research Station, Bessie, Oklahoma, 1999–2000.

Variable	Percent contribution values	
	May ^a	Aug ^b
Light intensity (lux)	20.3	9.5
Time of day (hours)	18.5	24.5
Year 2000	12.0	NA
Wind speed (m/s)	11.8	13.7
Litter depth (mm)	5.4	5.1
Shrub cover (%)	4.5	4.5
No grazing ^c	4.5	4.2
Visual obstruction (m)	4.3	9.4
Grass cover (%)	3.3	3.7
Year 1999	3.1	NA
Moderate ^c	2.9	5.5
Bare ground (%)	2.8	1.3
Screening cover ^d	2.0	2.6
Litter (%)	1.9	3.9
Forb cover (%)	1.4	1.9
Heavy ^c	0.9	4.9
Soil moisture (%)	0.6	5.5

^a May neural network model included data from 1999–2000.

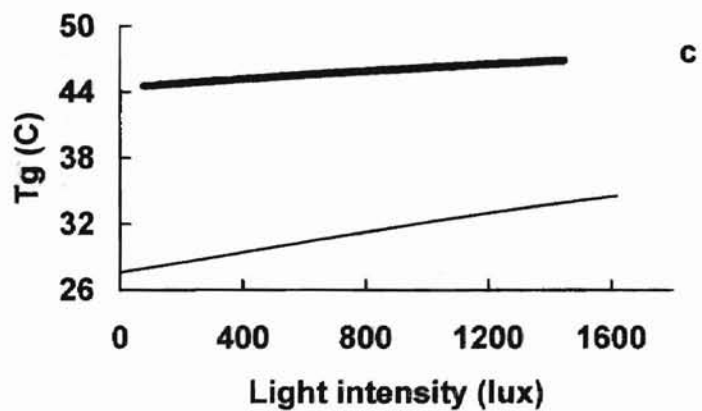
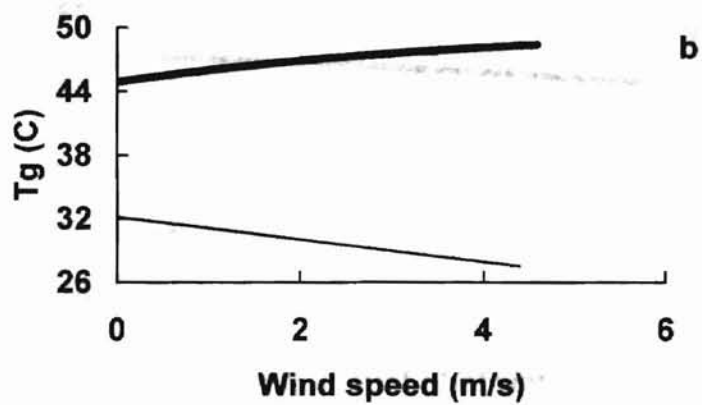
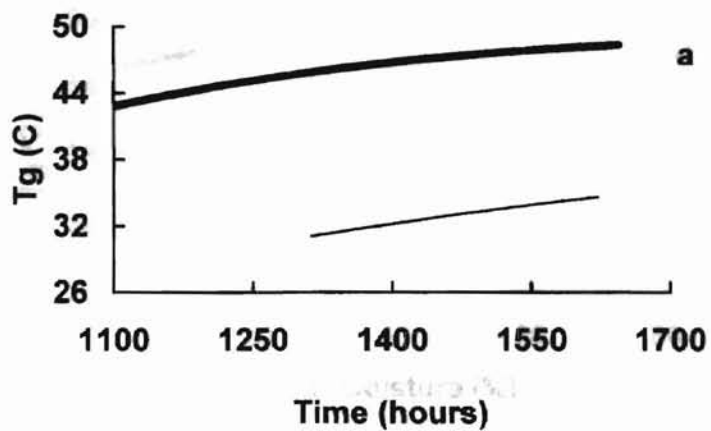
^b Aug neural network model included data from 2000.

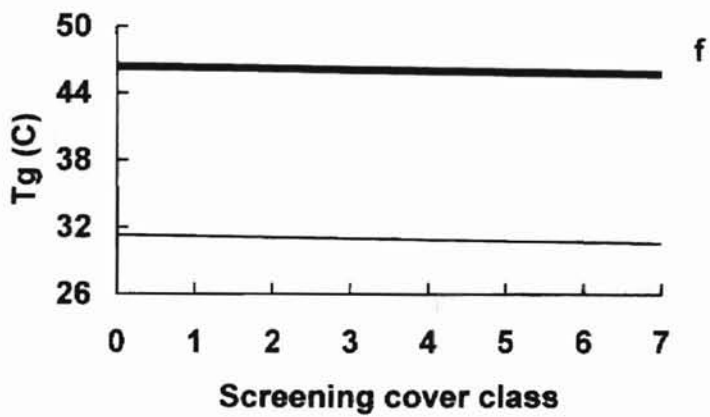
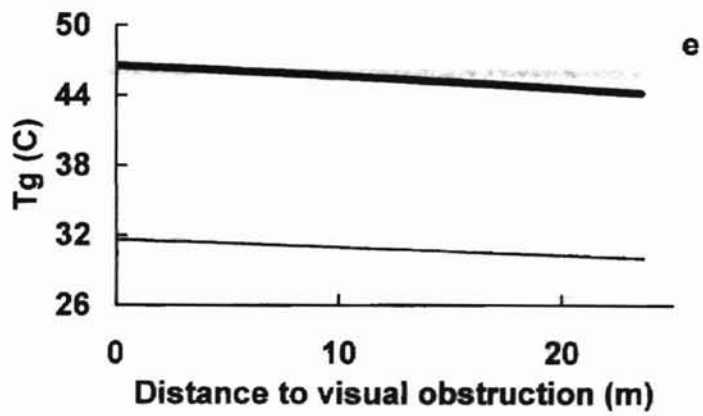
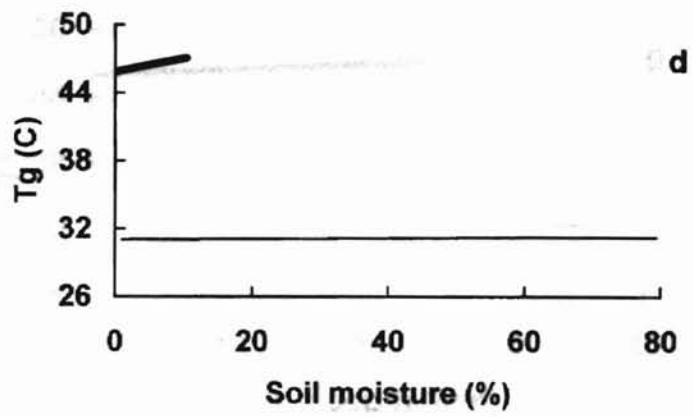
^c One of 3 grazing treatments included in the model.

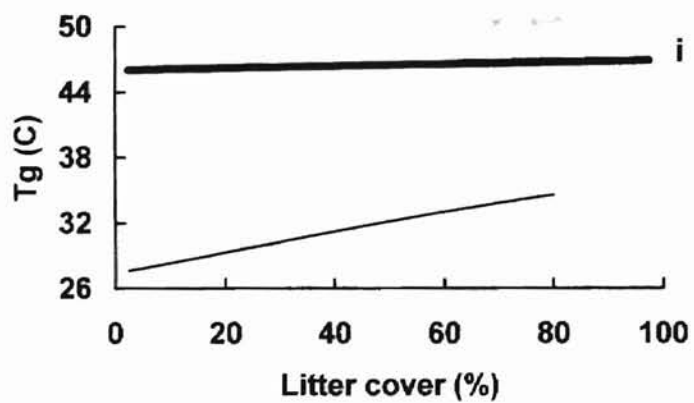
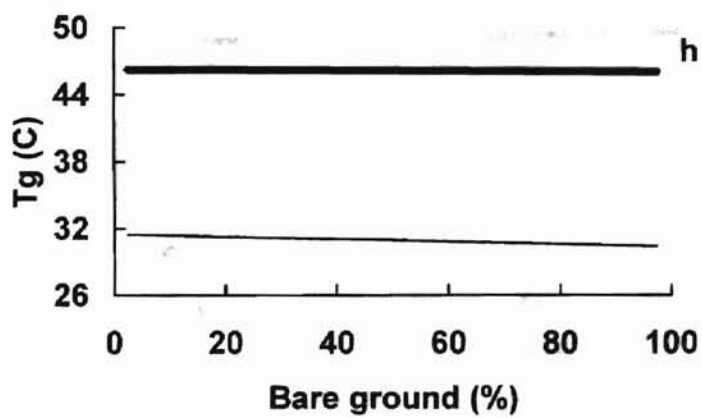
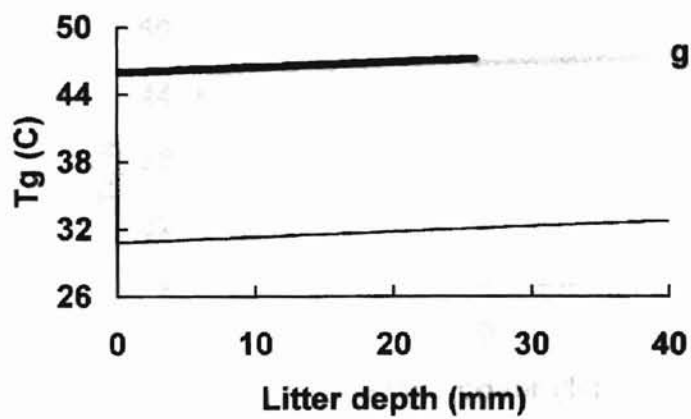
Table 5. Continued.

^d I used screening cover class from the fourth stratum (30–40 cm) because it had the highest component loading within factor one which explained 51.2% of the total variance.

Fig. 4. Relationships between mean habitat features and ground temperature ($^{\circ}\text{C}$) taken from the Marvin Klemme Experimental Range Research Station, Bessie, Oklahoma 1999–2000, generated from 2 artificial neural network models. Light lines were used to designate pre-growing season data (May) and bold lines were used to designate post-growing season data (Aug). Ground temperature was shown as a function of time of day (hours) (a), wind speed (m/s) (b), light intensity (lux) (c), soil moisture (%) (d), distance to visual obstruction (m) (e), screening cover class in the fourth stratum (30–40 cm) (f), litter depth (mm) (g), bare ground (%) (h), litter cover (%) (i), grass cover (%) (j), forb cover (%) (k), and shrub cover (%) (l).







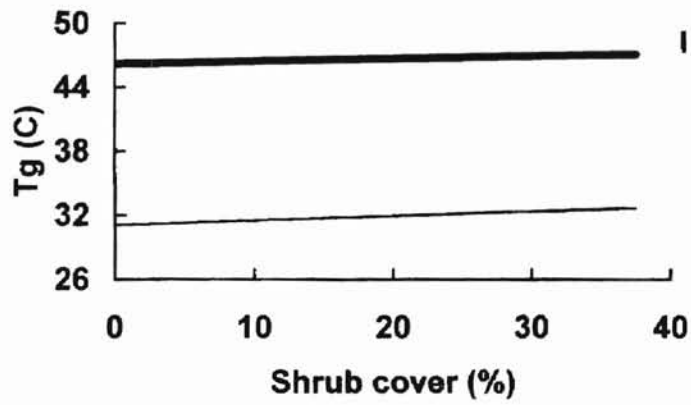
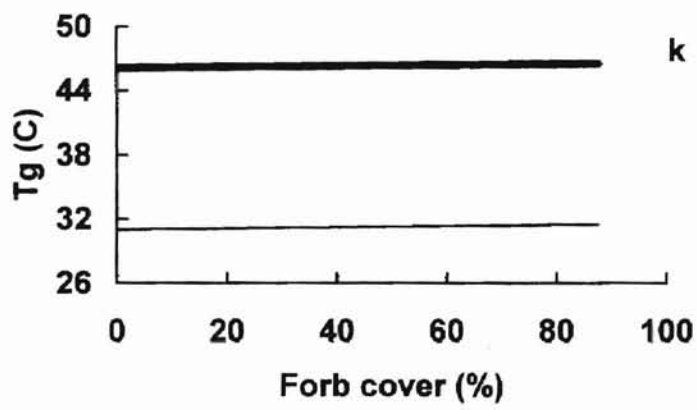
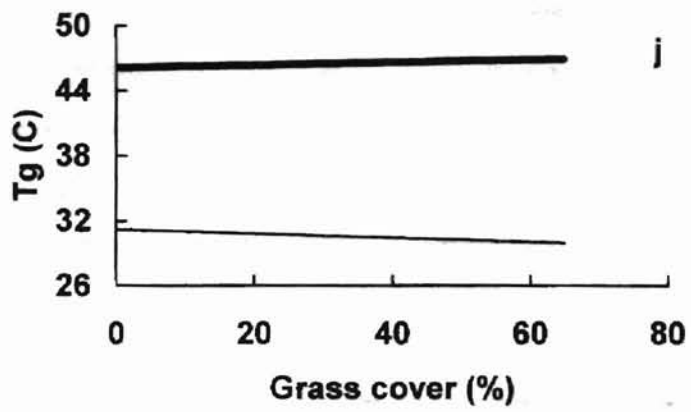


Table 6. Annual precipitation (mm), growing season (Apr–Sep) precipitation (mm), and growing season precipitation as a percentage of annual precipitation from weather data collected at the Marvin Klemme Experimental Range Research Station, Bessie, Oklahoma, 1999–2000 adapted from Gillen et al. (2000).

Year	Annual	Growing Season (Apr–Sep)	Growing Season as Percent of Annual Precipitation ^a
1990	670	514	76.7
1991	733	535	73.0
1992	774	484	62.5
1993	709	496	70.0
1994	575	361	62.8
1995	1,195	935	78.2
1996	817	781	95.6
1997	885	585	66.1
1998	598	163	27.3
1999	725	482	66.5
2000 ^a	692 ^a	426 ^a	61.6 ^a

^a All values based on data collected through September of 2000.

Table 7. Growing season precipitation (mm) at the Marvin Klemme Experimental Range Research Station, Bessie, Oklahoma, 1998–2000, adapted from Gillen et al. (2000).

Month	1998	1999	2000
Apr	31.0	180.1	110.0
May	56.4	141.7	36.1
Jun	29.2	89.2	237.0
Jul	24.9	17.5	41.7
Aug	20.6	22.6	0.0
Sep	1.3	30.7	1.3

to microclimate features (i.e. bare ground, grass cover) already selected for future analyses, so including them would have defeated the purposes of this data reduction exercise.

Grazing intensity and year affected distance to visual obstruction, litter depth, percent bare ground, and percent litter (Table 2). Distance to visual obstruction increased with grazing intensity and was consistent between years. Within years, the relationship between grazing intensity and distance to visual obstruction varied by season. In 1999, distance to visual obstruction was higher at the end of the growing season, but in 2000 the relationship was just the opposite and distance to visual obstruction was lower at the end of the growing season. Litter depth was negatively related to grazing intensity and was consistent between years and growing seasons. Percent bare ground increased with grazing intensity and was also consistent between years and growing seasons. In general, litter cover was also negatively related to grazing intensity and was consistent between years and growing seasons.

Thermal Environment

Ground temperature was minimally affected by grazing intensity and only varied with grazing intensity during 2 months in 1999 (Table 3). However, I did not attribute these differences in ground temperature to grazing intensity. Ground temperatures did vary by year, especially during the first 2 months of the growing season (May--Jun). In 1999, mean ground temperatures at random points in both months were about 8°C hotter than in 2000. In July 1999, mean ground temperatures were about 3°C cooler compared to 2000. Finally, mean ground temperature in August 1999 was about 4°C hotter compared to August 2000.

Avian Data

Nest Vegetation.—Grazing intensity and year did not affect microclimate features of nests within bird species (Table 4). Therefore, all data were pooled by bird species for further analysis. Although grazing intensity affected vegetation structure and composition at random (heat grid) points (Table 2), birds did not appear to respond to grazing intensity so all vegetation data for random (heat grid) points were pooled for comparisons across bird species (Figs. 1a–i).

Distance to visual obstruction, litter depth, percent bare ground, percent litter cover, percent forb cover, and percent shrub cover were different between nest and random points within bird species (Figs. 1b, 1d–f, 1h–i). Lark sparrow (4.6 ± 0.7 m) and meadowlark (3.7 ± 0.9 m) nests had shorter average distances to visual obstruction (more cover) than random points (7.7 ± 0.3 m), whereas, common nighthawk (13.5 ± 1.3 m) nests had longer average distances to visual obstruction (more cover) compared to random points (Fig. 1b). Common nighthawk (1.0 ± 1.0 mm) and lark sparrow (3.0 ± 0.4 mm) nests had shorter average litter depths than random points (5.0 ± 0.5 mm) (Fig. 1d). Grasshopper sparrow (13.4 ± 3.5 %), lark sparrow (16.3 ± 2.9 %), and meadowlark (3.9 ± 1.4 %) nests had less bare ground than random points (34.3 ± 1.8 %) on average, whereas, common nighthawk (65.0 ± 7.6 %) nests had more bare ground than random points on average (Fig. 1e). Common nighthawk (4.6 ± 1.4 %), lark sparrow (10.9 ± 1.5 %), and mourning dove (12.5 ± 2.2 %) nests had less litter cover than random points (24.5 ± 1.3 %) (Fig. 1f). Lark sparrow nests (8.7 ± 1.3 %) had less forb cover than random points (16.2 ± 0.8 %) (Fig. 1h). Finally, lark sparrow (43.3 ± 4.2 %) and mourning dove (20.5 ± 5.9 %) nests had more shrub cover than random points on average (3.6 ± 0.4 %) (Fig. 1i).

Nest site selection.—In 1999, mean maximum temperatures at nests of all species with adequate sample sizes for meaningful comparisons ($n > 1$ indicated by

solid vertical lines in Figs. 2, 3), except grasshopper sparrows, were cooler than random points (Figs. 2a,2c,2e,2g) In 2 of the 4 months (July and August) sampled in 1999, maximum temperatures at nests of at least one species were also obviously different from random points and did not require statistical verification (lark sparrow in Fig. 2e, and mourning dove in Fig. 2g). The distribution of bootstrap means at random points almost always exceeded 39°C, except during July 1999 when the left tail slightly overlapped 39°C

In 2000, maximum temperatures at nests with meaningful sample sizes for comparison were cooler than random points most of the time with 3 exceptions (Figs. 2b, 2d, 2f, 2g). In May, maximum temperatures at grasshopper sparrow nests were warmer compared to random points (Fig. 2b). In June, maximum temperatures at mourning dove nests were also warmer compared to random points (Fig. 2d). In July, maximum temperatures at common nighthawk nests were not different from random points (Fig. 2f). In all months except May, maximum temperatures at nests of at least one species were obviously different from random (lark sparrow in Fig. 2d, grasshopper and lark sparrows in Fig. 2f, and mourning doves in Fig. 2h), making statistical verification unnecessary. The distribution of bootstrap means at random points included 39°C through June, but excluded it afterwards.

In 1999, the proportion of time $>39^{\circ}\text{C}$ ($p >39^{\circ}\text{C}$) for nests of species with meaningful sample sizes for comparison ($n > 1$ as indicated by solid vertical lines) was always less at nests compared to random points (Figs. 3a, 3c, 3e, 3g). Only the bootstrap means for grasshopper sparrow nests in May were obviously different from random points (Fig. 3a), making statistical verification unnecessary. In May, ground temperatures at grasshopper sparrow nests never exceeded 39°C (Fig. 3a). In June, ground temperatures at the grasshopper sparrow nest exceeded 39°C for 22% of the 30-

hour sampling period or 4.22 hours each day (Fig. 3c). In July, ground temperatures at lark sparrow nests never exceeded 39°C (Fig. 3e). During the same month, ground temperatures exceeded 39°C at the mourning dove nest for 1.15 hours each sampling day, and 1.19 hours each sampling day at meadowlark nests. In August, ground temperatures exceeded 39°C at mourning dove, grasshopper sparrow, common nighthawk, and meadowlark nests for 5.84 hours, 5.95 hours, 6.37, and 6.52 hours during each sampling day, respectively.

In 2000, the proportion of time >39°C was not consistently lower at nests with meaningful sample sizes for comparison ($n > 1$) compared to random points (Figs. 3b, 3d, 3f, 3h). The proportion of time >39°C at nests was only obviously less compared to random points in May (lark sparrow and mourning dove nests in Fig. 3b) and June (all species in Fig. 3d), making statistical testing unnecessary. In May, the proportion of time >39°C at grasshopper sparrows was greater compared to random points (Fig. 3b). In July and August, the proportion of time >39°C was never less at nests compared to random points (Fig. 3f, 3h). In May, ground temperatures at mourning dove and lark sparrow, common nighthawk, and grasshopper sparrow nests exceeded 39°C for 0.03 hours, 0.76 hours, and 1.42 hours per sampling day, respectively (Fig. 3b). In June, ground temperatures at nests of all species never exceeded 39°C (Fig. 3d). In July, ground temperatures exceeded 39°C at common nighthawk nests for 4.4 hours during each sampling day (Fig. 3f).

Neural Network Model

I optimized performance of the neural model with data from May in both years by using 1 neuron and 1,500 iterations. The model explained 78.2% of the variation in the training data and 75.2% of the variation in the test data. The most important predictors of ground temperature were light intensity, followed by time of day, wind speed, and the

year 2000 (Table 5). Year was added as a variable in the neural models because of fluctuations in precipitation and temperature between years that may have contributed to the unusual patterns I observed. In subsequent simulations, ground temperature was positively related to time of day (Fig. 4A), light intensity (Fig. 4C), soil moisture (Fig. 4D), litter depth (Fig. 4G), litter cover (Fig. 4I), forb cover (Fig. 4K), and shrub cover (Fig. 4L). Ground temperature was negatively related to wind speed (Fig. 4B), distance to visual obstruction (Fig. 4E), screening cover (Fig. 4F), percent bare ground (4H), and grass cover (Fig. 4J).

I optimized performance of the neural model with August 2000 data by using 2 neurons with 2,000 iterations. The model explained 75.1% of the variation in the training data and 63.4% of the variation in the test data set. The most important predictors of ground temperature were time of day, followed by wind speed, light intensity, and distance to visual obstruction (Table 5). Ground temperature was positively related to time of day (Fig. 4A), wind speed (Fig. 4B), light intensity (Fig. 4C), soil moisture (Fig. 4D), litter depth (Fig. 4G), litter cover (Fig. 4I), grass cover (Fig. 4J), forb cover (Fig. 4K), and shrub cover (Fig. 4L). Ground temperature was negatively related to distance to visual obstruction (Fig. 4E), screening cover (Fig. 4F), and percent bare ground (Fig. 4H).

DISCUSSION

My goal was to evaluate the effects of grazing intensity on the thermal environment for ground-nesting birds in mixed-grass prairies of Oklahoma. Specifically, my objectives were: 1) to investigate the effects of grazing intensity on microclimate features, 2) to evaluate the effects of grazing intensity on ground temperatures, 3) to investigate the effects of thermal regimes on nest site selection for ground-nesting grassland birds, and 4) to create a model to determine which variables were the most important for predicting ground temperatures. To address the first objective, I compared

microclimate features (e.g. percent bare ground, distance to visual obstruction) at random points among 3 grazing intensities during 2 seasons each summer. To address the second objective, I compared mean ground temperatures at random points among three grazing intensities during 4 months of each summer. To address the third objective, I compared maximum ground temperatures and the proportion of time $>39^{\circ}\text{C}$ at nests compared to random points during 4 months of each summer. To address the final objective, I created 2 separate neural models to predict ground temperatures at the beginning and end of the breeding season based on microclimate and thermal variables.

Effects of Grazing Intensity on Microclimate Features

Microclimate features affected by grazing intensity in this study closely matched my expectations and results of other grazing studies (Table 2). For example, distance to visual obstruction, which is also a measure of cover (longer distance means less cover), generally increased with grazing intensity, as I expected. Sims et al. (1978) reported similar results at all 3 of the mixed-grass prairie sites (i.e. Cottonwood, Dickinson, and Hays) included in their study. Litter depth and cover also decreased with grazing intensity, as expected. Several researchers have found similar results at sites in Kansas, South Dakota, and Oklahoma, respectively (Tomanek and Albertson 1953, Coppock et al. 1983, Gillen et al. 2000). Finally, percent bare ground increased with grazing intensity, which I also expected. These results are consistent with the findings of Baker and Guthery (1990) on clay soils in South Texas, although they noted the effect varied by soil type.

Distance to visual obstruction is a biologically important variable for quantifying vegetation structure and height across plant community types for birds (Robel et al. 1970). In this study, I expected the distance to visual obstruction to increase with grazing intensity as livestock consumed more of the available forage. I also expected the distance to visual obstruction to decrease with time during the growing season as

precipitation peaked and stimulated new growth during the growing season. Although the patterns I observed between grazing intensity and distance to visual obstruction were consistent with my expectations, the patterns between time of the growing season and distance to visual obstruction were not consistent with my expectations between years (Table 2).

The pattern I observed between distance to visual obstruction and time during the growing season was not consistent between years, as I had originally expected. In 1999, distance to visual obstruction increased with time during the growing season (i.e. from May to August), but during the following year (2000) the relationship was just the opposite. These differences in trend during the growing season may have been due to interannual variation in the timing and amount of precipitation, which might have affected annual net primary production. Milchunas and Lauenroth (1993) showed that precipitation and annual net primary production (as measured by standing crop) were highly correlated on grassland sites across the globe in their exhaustive study. Other research on our study site has shown that live standing crop was independent of grazing intensity, but sensitive to years with favorable (above average) precipitation (Gillen et al. 2000). The growing season of 1999 followed the driest growing season during the last decade (+ 33.8% change from 1998) with growing season precipitation (Apr–Sep) comprising 27.3% of annual precipitation (Table 6). Conversely, the growing season of 2000 followed a more favorable year with precipitation during the growing season comprising 66.5% of annual precipitation. Peak precipitation in 1999 (April) occurred 2 months earlier and was about 76% of peak monthly precipitation (June) in 2000 (Table 7). This shift in precipitation peak and amount may have delayed plant production, creating more plant cover closer to the end of the summer. I believe the unusually dry year in 1998 best explains the unexpected increase in distance to visual obstruction at the end of the growing season during the growing season of 1999.

Litter depth is also a biologically important variable because it relates to the amount of residual and decaying vegetation present on a landscape, which is particularly important for many ground-nesting birds that rely on this substrate for nest placement and construction (Hansell 2000). In this study, I expected litter depth and cover to decrease with grazing intensity and time during the growing season as hoof action and increased temperatures promoted decomposition and microbial activity (Samson and Knopf 1996).

The results presented here were consistent with my expectations and the trends in other studies (Tomanek and Albertson 1953, Sims et al. 1973). Mean litter depth and percent litter cover both decreased with grazing intensity and time during the growing season, as expected (Table 2). Specifically, results from this study showed that the absolute magnitude of change between litter variables in the no grazing and moderate grazing treatments were largest. Sims et al. (1973) found similar patterns at moderately grazed (Hays) and 2 heavily grazed (Dickinson and Cottonwood) mixed-grass prairie sites, where they reported nearly 5-times more litter biomass on grazed compared to ungrazed sites. Data from my study didn't show differences greater than 2-fold between no grazing and moderate grazing treatments, but did follow the general trend that Sims et al. (1973) reported. The difference in magnitude that Sims et al. (1973) reported probably was larger than what I reported because the majority of their study sites were near the northern extreme of the mixed-grass prairie association where precipitation is higher.

Results from my data on percent bare ground were not entirely consistent with my expectations. I expected percent bare ground to increase with grazing intensity as livestock consumed more forage, thereby creating more open or bare spaces. I also expected percent bare ground to decrease with time during the growing season as precipitation stimulated new growth. My results were consistent with the first

expectation, but not the second. Percent bare ground increased with grazing intensity in both years, as expected, but decreased with time during the growing season in 1999. I suspect this result was also an artifact of an unusually dry period during the preceding growing season (Tables 6, 7). Following the dry year of 1998, the plant community may have been recovering after an unusually dry growing season punctuated by an abnormal pulse of precipitation in October. Baker and Guthery (1990) found similar results in Texas, but noted these effects were influenced by soil type. In their study, percent bare ground was 3-times higher ($17 \pm 3.3\%$ vs. $5.1 \pm 0.8\%$) on heavily grazed compared to moderately grazed clay soils. The magnitude of difference in percent bare ground on heavily grazed versus moderately grazed sites at my study site was smaller (Table 2), especially during the summer of 2000. I suspect the differences in magnitude of percent bare ground between sites could have been a result of grazing time (continuous in Texas, Apr-Sep this study), assuming stocking rates were similar, or differences in plant community composition.

Effect of Grazing Intensity on Ground Temperature

I expected ground temperature to increase with grazing intensity and time. Furthermore, I expected the no grazing treatment to be coolest, followed by the moderately, and heavily grazed treatments, respectively. In general, the patterns I observed were mostly consistent with these predictions during the first 2 months of the summer (May--Jun), but not necessarily during the last 2 months (Jul--Aug) (Table 3). The unexpected result during the first half of the summer occurred in May 1999, when ground temperature decreased with grazing intensity. However, I attribute these results to the confounding effects of weather variation between sampling days. Weather data collected on the site showed ambient temperatures were similar across days, but showed 2-fold differences in maximum wind speed (18 vs. 8 m/s) and solar radiation (16.07 vs. 28.52 MJ/m²). In desert grasslands, Wolf and Walsberg (1996) showed that

increasing wind speed from 0.4 m/s to 3.0 m/s while holding solar radiation constant, produced an effect equivalent to reducing air temperature by 11°C. These results showed the effects of wind speed on temperature and emphasized the role that higher wind speeds played in decreasing heat loads for birds. Higher wind speeds recorded on my first sampling day in May could have produced a larger cooler effect than wind speeds on the subsequent day, thereby lowering ground temperatures disproportionately.

The negative relationship between ground temperature and grazing intensity in 1999 may relate to the effects of litter depth on heat flow in the canopy. I expected ground temperature to increase with grazing intensity as plant cover was removed, but other authors have shown this relationship may not exist in tallgrass prairies, which the no grazing treatment in this study most closely resembled. In central Oklahoma, canopy air temperature (10 cm) and leaf temperature were higher in ungrazed, unburned sites (high fuel) compared to moderately grazed, unburned (low fuel) sites in midafternoon (Ewing and Engle 1988). Although the authors were primarily interested in comparisons between burned and unburned plots, differences in temperature between ungrazed and moderately grazed plots were similar to results in this study. Ewing and Engle (1988) attributed their results to the moderating effects of litter in the ungrazed pasture. Results from neural modeling in this study showed similar results (Fig. 4) and provided more evidence that litter levels may contribute to heat loading.

Effects of Microclimate Features on Nest Site Selection

I have already shown that grazing intensity affected microclimate features at random points (Table 2), but did not affect those same features at nests (Table 4). Therefore, avian species appear to respond to vegetation cues, but do so independent of changes in microclimate features caused by grazing intensity. I interpret this result to

mean that avian species select nest sites with similar vegetation structure and composition regardless of grazing intensity or year.

Although distance to the nearest woody plant was not different between nests and random points for any species, this variable separated species based on their flexibility to choose nest sites (Fig. 1a). Meadowlarks (297.4 ± 206 vs. 117.8 ± 22.1 mm) and lark sparrows (7.5 ± 3.6 vs. 117.8 ± 22.1 mm) were most sensitive to distances to the nearest woody plant, as indicated by the absolute difference in mean values at nest compared to random points. Both of these species had narrow nest site requirements and primarily selected the same nest substrate regardless of site or grazing treatment. For example, on my site, 98% ($n = 47$) of all lark sparrow nests were in broom snakeweed shrubs. The remaining nest was placed at the base of an acacia (*Mimosa* spp.) shrub (K. Suedkamp, unpublished data). Results from other studies indicated that proximity to shrubs might be important for copulation behaviors in this species (Martin and Parish 2000). Lark sparrows are unique among passerines in that males typically pass females a twig during copulation and immediately prior to choosing a nest site. In areas like my study site, where shrubs are not abundant or well distributed across the landscape, proximity to shrubs might serve as the necessary cue for nest site selection in lark sparrows. All meadowlark nests ($n = 9$) on my site were located in grass clumps, which indicated narrow nest site requirements and little flexibility in nest site selection for this species as well. Results from other studies reported that nest sites were dominated by grass cover >80% (Kershner and Bollinger 1996). Other studies in Illinois also reported that percent live vegetation and mean grass height were the most important predictors of meadowlark abundance (Herkert 1994). These combined results suggest that grass cover (both alive and dead) may be the most important cue for nest site selection in meadowlarks.

Distance to visual obstruction did vary by species when compared to random points (Fig. 1b). Common nighthawks (13.5 ± 1.3 vs. 7.7 ± 0.3 m), followed by meadowlarks (3.7 ± 0.9 vs. 7.7 ± 0.3 m), and lark sparrows (4.6 ± 0.7 vs. 7.7 ± 0.3 m) were most sensitive to distance to visual obstruction, as indicated by the absolute difference in means at nests compared to random points. Meadowlark and lark sparrow nests had more cover (shorter distance to visual obstruction) than random points, which indicated that adequate cover was a necessary requirement for nest site selection in these species. Results from other studies discussed in the previous paragraph support this assertion and showed that meadowlark and nest sites were both associated with taller cover, particularly by grasses (Herkert 1994, Lanyon 1995, Kershner and Bollinger 1996). Common nighthawk nests had less cover (longer distance to visual obstruction) than random points, indicating the importance of bare ground in nest site selection. The differences in nest site characteristics described indicate that meadowlarks and common nighthawks have different nesting strategies. For meadowlarks, the presence of taller grasses is important for providing shelter from predators (Lanyon 1995), whereas, the absence of cover at common nighthawk nests makes the use of cryptic egg coloration necessary to avoid predators (Poulin et al. 1996).

Both litter variables (depth and percent cover) were different at common nighthawk and lark sparrow nests compared to random points (Fig. 1d), but only percent litter cover was different at mourning dove nests compared to random points (Fig. 1f). Litter depth and percent litter cover were both less at nests of common nighthawks and lark sparrows, indicating the importance of minimal dead material around potential nest sites. I believe these results are related to the importance of bare ground at potential nest sites for both species. For common nighthawks, minimal litter depth and cover were probably associated with bare ground, which was the primary nest substrate for

this species on my site (K. Suedkamp, unpublished data). For lark sparrows, minimal amounts of litter around nest sites may have been important for providing foraging opportunities for this ground- leaning species (Ehrlich et al. 1988).

Percent bare ground at nests of common nighthawks, grasshopper sparrows, lark sparrows, and meadowlarks were different from random points, as expected. I expected species that require bare ground for nest sites or foraging would select nest sites with higher amounts of bare ground than random points. My data were consistent with this prediction and showed that common nighthawk nest sites were the second most sensitive to bare ground (65 ± 7.6 vs. 34.4 ± 1.8 %), as indicated by the absolute difference between the nest mean compared to random points. Likewise, I expected species that were highly sensitive to cover, such as meadowlarks, to have less bare ground at nest sites compared to random. The patterns in my data were consistent with this expectation and show that meadowlarks were the most sensitive to bare ground (3.9 ± 1.4 % vs. 34.4 ± 1.8 %) (Fig. 1e). Authors in Illinois have documented similar results and reported that meadowlark nests sites had no bare ground, but random points had 4.2% bare ground on average (Kershner and Bollinger 1996). The extreme sensitivity of meadowlark to bare ground shown in my data, indicate this variable might provide an important cue during nest site selection in this species. Finally, mean amounts of bare ground at nests of grasshopper sparrow and lark sparrows were also less compared to random points, indicating these species were more sensitive to bare ground than originally expected.

The relatively small amount of bare ground at nests of all species except the common nighthawk might be a result of thermoregulatory constraints imposed by a lack of plant cover for shelter associated with increasing amounts of bare ground. These thermoregulatory constraints were probably most severe for common nighthawks

because they usually nested directly on bare ground (K. Suedkamp, unpublished data). Eppley (1996) suggested that thermal stress might act as a selective agent on avian reproduction by favoring those species that develop thermal independence earlier. Nice (1962) suggested that altricial species might become thermally independent earlier than precocial species due to their shorter development times. If these assertions are true, temperature may have influenced development patterns in nighthawks by favoring early locomotion instead of thermal independence.

Based on my results for proximity to woody homologs, I expected the species that nest in woody plants to be clearly separated from those that rely on grass clumps for nest substrates. However, the patterns in my data were not as clear as I expected. Lark sparrows nested almost exclusively in broom snakeweed during this study, so I expected them to be particularly sensitive to shrub cover. In fact, my results showed that lark sparrows were the most sensitive to percent shrub cover around nest sites (43.3 ± 4.2 vs. 3.6 ± 0.4 %). The magnitude of sensitivity to this variable shown in my study, indicated that shrub cover was probably the most important cue measured for nest site selection in this species. The association of lark sparrows with shrubs reported by Martin and Parrish (2000) may be related to shelter from thermal extremes that shrubs may provide. If results from the neural models (Table 5) are accurate, then shrubs may moderate extreme temperatures more efficiently than grasses or forbs. Mourning doves were also sensitive to shrub cover (20.5 ± 5.9 vs. 3.6 ± 0.4 %), although not nearly to the degree that lark sparrows showed. On my study site, mourning doves often selected nest sites that were sheltered by broom snakeweed, indicating shrubs may have been important for sheltering eggs from predators or excessive heat loads later in the summer. Protection from excessive heat loads later in the summer may be particularly

important because this species is the only species I have discussed that breeds into August at this site (K. Suedkamp, unpublished data).

Effects of Ground Temperature on Nest Site Selection

Maximum ground temperatures at nests of species with adequate sample sizes ($n > 1$ as indicated by solid vertical line in Fig. 2) were mostly less compared to random points during both breeding seasons with a few exceptions. Sample size within species was inadequate for comparison during several months, so I will limit discussion to those species with adequate sample sizes for comparison ($n > 1$) to draw meaningful conclusions. In May 2000, mean maximum temperatures at mourning dove nests were 1.5°C less compared to random points (Fig. 2b), indicating ambient temperatures were greater than optimal incubation temperatures. Webb (1987) reported that optimal incubation temperatures for mourning doves ranged from 35°C to 37°C , so it is not surprising that mourning doves selected nest sites that created maximum temperatures that were cooler than random points. In May of both years, mean maximum temperatures at grasshopper sparrow nests ranged from 1.35°C to 2.15°C greater than random points, indicating ambient temperatures may have been below optimal incubation temperatures. Research by Webb (1987) supports this hypothesis and showed that mean incubation temperature for 36 species of passerines was 32.2°C , which was greater than maximum daily temperatures during May by about 4°C on average (Oklahoma State University, Oklahoma climatological survey mesonet data, 1990--2000). I interpret these results to indicate that grasshopper sparrows selected nest sites early in the breeding season (May) because they were warmer than random points and closer to optimal incubation temperatures.

In June, mean maximum temperatures at nests were not always lower at nests compared to random points (Fig. 2d). For example, mourning dove nests were warmer

than random points, but this difference was small (0.08°C). Even though mean maximum temperature was based on 2 nests in this case, the difference could have been due to variation in sampling or daily weather patterns independent of nest site selection. Due to the potential effects of variation on weather conditions (i.e. solar radiation, wind) discussed previously, I am unable to attribute this difference to nest site selection by mourning doves. Mean maximum temperatures at lark sparrow nests were lower than random points by 2.0°C , indicating this species selected nest sites that were also cooler than random points. Mean maximum temperatures at lark sparrow nests (33.87°C) were close to the optimal incubation temperature reported for passerines (32.2°C) (Webb 1987). I believe the similarity in mean maximum temperatures at nests and those required for optimal incubation indicate lark sparrows may have a narrower thermal tolerance than the other passerine I studied (grasshopper sparrow). If this hypothesis is true, it makes sense that lark sparrows would select nest sites that maintain tighter temperature control, especially during June, which may be important for multiple nest attempts.

In July, meadowlarks and lark sparrows were the only species with mean maximum temperatures at nests that were lower than random points (Fig. 2e). Although the difference was small (0.68°C) at meadowlark nests, mean maximum temperatures at nests were maintained around critical levels (39°C) reported for optimal survival for many birds (Webb 1987, Guthery et al. 2000). Although I found a limited number of meadowlark nests, construction of the nests I found were generally more elaborate than the other species (K. Suedkamp, unpublished data). Although I lack sufficient data to confirm this hypothesis, I suspect that the complete roof and entrance usually present play a large role in moderating thermal loads for this species.

In August, only nests of mourning doves, lark sparrows, and common nighthawks were cooler than random points (Fig. 2g-h). However, these results are somewhat suspect because I only observed mourning doves nesting into August on my site (Ken Suedkamp, unpublished data). There is the possibility that I never observed lark sparrows and common nighthawks nesting in August because I wasn't looking for them, but reports of nesting attempts this late in the breeding season are rare, especially in southern location (Poulin et al. 1996, Martin and Parrish 2000). Even if these species were no longer utilizing nest structures, mean maximum ground temperatures around nest sites selected throughout the breeding season indicate lethal temperatures capable of killing adult birds were present (Goldstein 1984).

The proportion of time $>39^{\circ}\text{C}$ in May of both breeding seasons was not consistently lower at nests compared to random points, especially for grasshopper sparrows. In May 1999, grasshopper sparrow nests never exceeded 39°C , but did exceed this critical value in May 2000. The sample size for grasshopper sparrow nests in 2000 ($n = 4$) was twice that in 1999 ($n = 2$), which leads me to believe the patterns observed in 2000 were more reflective of true nest site selection and less dependent on sampling variation and size. Maximum temperatures and the proportion of time $>39^{\circ}\text{C}$ at grasshopper sparrow nests in May both lead me to believe that this species may select warmer nest sites earlier in the breeding season, especially during cool months like May 1999. day.

In June 2000, ground temperatures at nests of lark sparrows and mourning doves never exceeded 39°C (Fig. 3d). These results indicate unusual cool periods, such as June 2000, may have been particularly important for multiple nesting attempts. According to the mean proportion of time $>39^{\circ}\text{C}$ at random points, the breeding season of 2000 was warmer in May, but cooler in June compared to the previous summer. If

ambient temperatures provide cues for multiple nesting attempts, then females may have attempted additional clutches due to the unusually cool weather in June 2000. Work done by Meijer et al. (1999) on European starlings (*Sturnus vulgaris*) in Germany supported this hypothesis and reported that low temperatures during early spring delayed egg laying. These authors concluded that the sensitivity of reproduction to spring temperatures served as an adaptation by timing egg laying and the rearing of young with periods of high food production. If these hypotheses are true, then climatic fluctuations may alter the timing of breeding in southern portion of the Great Plains, but future research on the response to cool temperatures later in the breeding season is needed.

In July, the proportion of time $>39^{\circ}\text{C}$ at nests was not consistently lower compared to random points (Figs. 3e-f). In July 1999, mean temperatures at nests of meadowlarks exceeded 39°C for about 1.2 hours each sampling day, whereas, random points exceeded 39°C for about 1.6 hours each sampling day. These results indicate that nest sites selected by meadowlarks maintained temperatures below critical levels for 0.30 hours longer than random points. If the intensity of these periods were sufficient to cause lethal effects, 0.30 hours might be important. Webb (1987) showed that most birds subjected to temperatures $>40^{\circ}\text{C}$ for limited duration or continuous exposures were not able to tolerate these heat loads. The proportion of time $>39^{\circ}\text{C}$ at nests of common nighthawks was greater than random points in July 2000, indicating shelter or other heat avoidance mechanisms would be necessary to avoid overheating. The use of bare ground as a nest substrate by this species indicates that thermoregulatory constraints later in the breeding season may have favored developmental strategies that serve as adaptations for avoiding lethal temperatures. The ability of chicks in this precocial species to be mobile and gain thermal independence at earlier stages may enable

nestlings to move out of direct sunlight and thereby avoid exceeding critical temperatures (Fowle 1946, Poulin et al. 1996). The presence of a large mouth in relation to body surface area might also serve as a cooling mechanism when ambient temperatures exceed 42°C (Cowles and Dawson 1951).

In August, mean temperatures at nests of mourning dove and common nighthawks exceeded critical temperatures less than random points (Fig. 3g). However, I will only discuss the results from mourning doves because I never observed common nighthawks nesting in August (K. Suedkamp, unpublished data). Mourning doves are unique among the birds I studied because they were the only species I ever observed nesting this late in the breed season, often with eggs as late as August 15 (K. Suedkamp, unpublished data). The length of the breeding season in this species makes the ability to maintain relatively constant temperatures during incubation important, especially in southern regions (Baskett et al. 1993). Even though other authors have documented nesting through October in surrounding states (Baskett et al. 1993), I expect peak activity would be adjusted to compensate for increasing temperatures. Research done by Geissler et al. (1987) supports this hypothesis and showed that nesting activity in the southern portion of the Central Management Area peaked in late April to early May, and then declined throughout the remainder of the breeding season. Data from my study were consistent with the patterns reported from this region (Geissler et al. 1987, Baskett et al. 1993) and showed that 53% ($n = 9$) of nests were found in May, compared to 29% ($n = 5$) in June, and 18% in August ($n = 3$) (K. M. Suedkamp, unpublished data).

Artificial Neural Network Models

I constructed 2 models for predicting ground temperature because of the differences in sampling regimes between vegetation and thermal measurements. Although I measured thermal variables monthly from May to September in both years, I

measured vegetation variables once at the beginning of the growing season (May) and once at the end of the growing season (Aug). Although I could have pooled these 2 data sets, my results indicated that several confounding factors might have affected the results. The largest confounding effect was the positive relationship between time (time of day and season) and ground temperature that occurred independent of any treatment that I superimposed. The percent contribution values for time of day and year showed the strong effects of this confounding factor. The second confounding effect was the unexpected relationship between cover and temperature in the no grazing pastures. Although this could be related to the confounding factor I just mentioned, it could also be the result of sampling error, or true patterns, but I am unable to separate these effects with any degree of confidence.

In general, relationships between the predictor and response variables were as expected with 3 exceptions. I expected wind speed to be negatively related to ground temperature, but this relationship was positive in the May models. I suspect this result was related to the unexpected pattern of increasing temperature with more cover in the no grazing treatment, but I am unable to confirm this with my data. Although documentation of this type of relationship exists (Engle and Ewing 1988), these patterns have been found in tallgrass prairies, which most of this study site does not resemble. Further investigation in this area across a wider variety of grassland types is needed to confirm this pattern.

Secondly, I expected bare ground to be positively related to ground temperature, but simulations from the August model show the opposite trend (Fig. 4H). This result was counterintuitive and unlikely to represent true patterns. Data presented in this document show that bare ground was most abundant in heavily grazed treatments (Table 2), and that ground temperatures were usually hottest in heavily grazed treatments (Table 3). Therefore, this result was most likely an artifact of the sampling

technique. I measured percent bare ground by using a Daubenmire frame to estimate cover classes. In subsequent analysis, I used the midpoint of each class to plot the results, which were categorical in nature and not always reflective of the true amount of bare ground present.

Finally, I expected plant composition variables (% grass, forb, and shrub) to be negatively related to ground temperature because I assumed that more cover meant cooler temperatures. Grass cover was negatively related to ground temperature (Fig. 4J), but forb and shrub cover were both positively related to ground temperature in the May model (Figs. 4K–L). One possibility was that grass cover facilitated air movement, thereby decreasing ground temperatures. Data from simulations in the May model showed that litter was positively related to ground temperature (Fig. 4I), whereas, grass cover was negatively related (Figs. 4J). Simulation data suggest that live plant cover might have been more effective at dissipating temperature than dead plant material (litter), but I am unable to make definitive conclusions from my data.

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