Avian Behavior, Ecology, and Evolution

Experimental evidence that nest orientation influences microclimate in a temperate grassland

Evidencia experimental de que en un pastizal templado la orientación del nido influencia el microclima

Joanna L. Corimanya [1,2] (iD) , *Emma B. Smith* [1] (iD) and *W. Alice Boyle* [1] (iD)

ABSTRACT. Birds exhibit an assortment of behavioral strategies to cope with variable environmental conditions during reproduction, including altering nest construction behaviors. In species building enclosed domed nests, the microclimate within nests is influenced not only by its structure and the surrounding vegetation but also by the orientation of the nest opening. Many grassland-dependent birds build dome-shaped nests with clear directionality of openings. We studied two species in northeastern Kansas, United States that typically orient their nests east to northeast in this region. However, in a drought year, both Grasshopper Sparrows (*Ammodramus savannarum*) and Eastern Meadowlarks (*Sturnella magna*) shifted orientations of their nests southward toward prevailing winds. We hypothesized that this shift reduced the deleterious effects of heat stress on parents and developing young by diminishing morning solar radiation and increasing cooling due to the prevailing southerly winds. To test this hypothesis, we measured temperature, humidity, and wind speed at pairs of unoccupied, field-collected sparrow and meadowlark nests, experimentally placed to face south or east (control) in a non-drought year. Nest orientation affected the daily microclimate patterns, with south-facing nests warming later in the day relative to east-facing nests. The temperature differences depended upon humidity, with south-facing nests being relatively cooler under more humid conditions. This work provides the first experimental evidence of the benefits of plasticity in nest construction under challenging thermoregulatory conditions and shows how ground-nesting birds may reduce thermoregulatory demands during incubation under climate variation.

RESUMEN. Las aves exhiben una variedad de estrategias de comportamiento para hacer frente a las condiciones ambientales variables durante la reproducción, incluyendo la alteración de los comportamientos de construcción de nidos. En las especies que construyen nidos con forma de domo cerrado, el microclima dentro de los nidos está influenciado no sólo por su estructura y la vegetación circundante, sino también por la orientación de la abertura del nido. Muchas aves que dependen de los pastizales construyen nidos en forma de domo con una clara direccionalidad de las aberturas. Estudiamos dos especies en el noreste de Kansas, Estados Unidos, que típicamente orientan sus nidos de este a noreste en esta región. Sin embargo, en un año de sequía, tanto el Chingolo saltamontes (*Ammodramus savannarum*) como el Chirlobirlo (*Sturnella magna*) cambiaron la orientación de sus nidos hacia el sur, hacia los vientos predominantes. Hipotetizamos que este cambio redujo los efectos nocivos del estrés por calor en los padres y en los jóvenes en desarrollo, al disminuir la radiación solar matutina y aumentar el enfriamiento debido a los vientos predominantes del sur. Para probar esta hipótesis medimos la temperatura, la humedad y la velocidad del viento en pares de nidos desocupados de chingolos y chirlobirlos recolectados en el campo, colocados experimentalmente para estar orientados hacia el sur o el este (control), en un año sin sequía. La orientación de los nidos afectó los patrones microclimáticos diarios, con los nidos orientados al sur calentándose más tarde en el día, en relación con los nidos orientados al este. Las diferencias de temperatura dependieron de la humedad, siendo los nidos orientados al sur relativamente más frescos en condiciones más húmedas. Este trabajo proporciona la primera evidencia experimental de los beneficios de la plasticidad en la construcción de nidos bajo condiciones de termorregulación desafiantes y muestra cómo las aves que anidan en el suelo pueden reducir las demandas de termorregulación durante la incubación bajo la variación climática.

Key Words: *enclosed nest; Konza Prairie; nest architecture; nest construction; tallgrass prairie; thermal tolerance*

INTRODUCTION

Avian nest architecture functions to protect parents and young from predation (Mainwaring et al. 2014) and environmental stressors (Edwards et al. 2020) during incubation and brooding. The nest structure attenuates changes in egg temperature when the attending parent is absent and provides a thermal buffer to minimize parental energy expenditure when external temperatures are outside the species' thermoneutral zone (White and Kinney 1974). Reproducing birds must avoid heat stress while maintaining egg temperature for proper embryonic development (DuRant et al. 2013). Furthermore, parents must minimize the developmental costs of both cold and hot temperatures to

embryos during periods when they leave the nest (Webb and King 1983). Most songbirds (Passeriformes) utilize one of three types of nests: open-cup nests, cavity nests, or domed nests. Domed nests are enclosed, having a roof and an entrance on one side and are most common in the smallest passerines (Collias 1997). In grasslands, many birds nest on the ground, where they experience little protection from climatic extremes (Carroll et al. 2015). Whereas some taxa, such as nightjars (Ingels et al. 1984) and shorebirds (Tulp et al. 2012), lay their eggs in the open where parents and young are subject to the full brunt of solar radiation and storms, many ground-nesting birds build domed nests (Sutter 1997). Such species can modify the nest microclimate by changing

---

[1]Division of Biology, Kansas State University, [2]Department of Ecology and Evolutionary Biology, University of Kansas

their nests' structure, location, and orientation (Verbeek 1981; With and Webb 1993). Successful domed nests are associated with a favorable microclimate (Kim and Monaghan 2005). However, parental nest orientation decisions are not always adaptive and, sometimes, the preferred nest orientation leads to lower nestling fitness (Lloyd and Martin 2004). The optimal microclimate minimizes parental thermoregulatory costs while maximizing offspring growth potential (Mainwaring et al. 2014). Over long timescales, variation in orientation is thought to reflect adaptive responses to local climatic variation (Schaaf and de la Peña 2020). In ground-nesting species, domed nests may be advantageous because they are more inconspicuous than open cups, offering nesting birds increased protection from predation (Fulton 2019). Additionally, domed nests may protect parents and offspring from unfavorable weather conditions; the proportion of species building domed nests increases in hotter, more arid regions with less canopy cover (Duursma et al. 2018). Furthermore, parental foraging bouts are longer in domed nest-building species than open cup (Matysioková and Remeš 2018), consistent with reduced predation risk and buffered microclimate. Although comparative evidence suggests that the main advantage of domed nests is related to the thermal buffer they provide (Martin et al. 2017), few experimental tests of this hypothesis exist (Perez et al. 2020) and none so far have measured temperature, wind, and humidity using naturally constructed nests. Experimental tests of this hypothesis are especially relevant in the highly climatically variable Great Plains of North America.

Nest orientation influences the temporal pattern of heating and cooling within a domed nest due to the direction of the sun's path across the sky and the prevailing wind direction. During the breeding season in the northern hemisphere, the sun rises roughly in the east-northeast. Consequently, nests oriented eastward receive most of their solar input during cooler morning hours, and the domed roof provides shade during the hotter afternoon hours. Ground-nesting passerines at mid latitudes with domed entrances typically face their nests toward the east or northeast, but those breeding in warmer, low-latitude regions orient nests in a more northerly direction (Burton 2007). This pattern is consistent with morning warming being important in cooler climates and afternoon shading being necessary for hotter climates (Burton 2007). Similarly, in the southern hemisphere, interannual variation in nest orientation was related to mean temperatures, consistent with domed nest orientation being modulated to increase warming in cool years and minimize warming in warmer years (Schaaf and de la Peña 2020). In many species, nest orientation has a larger influence on reproductive success than habitat quality; however, this has yet to be tested experimentally in ground-nesting birds (Goodenough et al. 2008; Charter et al. 2010; Briggs and Mainwaring 2021). Deviations from broad geographic patterns in nest orientation may reflect local differences in prevailing wind direction, which would provide evidence of behavioral modification of nest microclimate in response to local conditions (Hartman and Oring 2003).

During the spring and summer months (i.e., the breeding season) in the tallgrass prairies of northeast Kansas, United States, birds experience high average daily temperatures accompanied by high relative humidity and prevailing winds from the south (Sugita and Brutsaert 1990; Burnette et al. 2010; Rahmani et al. 2015). In this region, the mean orientation of the two most common ground-nesting, grassland-dependent species (Grasshopper Sparrows, *Ammodramus savannarum,* and Eastern Meadowlarks, *Sturnella magna*) is toward the east and northeast, respectively (Hubbard et al. 2006). These orientations face away from southward prevailing winds and toward morning sun (Long et al. 2009). However, weather varies interannually, especially in mid-continental climates; this region is subject to periodic droughts associated with elevated temperatures (Mishra et al. 2010). In 2018, when northeast Kansas experienced one such drought, Grasshopper Sparrows and Eastern Meadowlarks shifted their nest orientations toward more southward and westward orientations (Smith et al., in press). Other studies in forests and grasslands have also documented nonrandom nest orientation and within-season shifts in nest orientation, hypothesizing that these patterns represent a plastic response to climatic variation (Burton 2006; Long et al. 2009; Landler et al. 2014; Schaaf et al. 2018).

We hypothesized that the drought-associated orientation shift in our system (and similar shifts observed in other studies) reflected behavioral choices by females that mitigated costs related to the hot, dry climatic conditions. We conducted an experimental study using real, enclosed bird nests to (1) directly test the consequence of nest orientation on nest microclimate, independent of other nest site selection choices that females make during nest building or their behavior post laying, and (2) determine the microclimatic factors most affected by orientation (i.e., temperature, humidity, or wind speed). Specifically, we predicted that south-facing nests would be cooler than east-facing nests due to reductions in morning solar radiation. We also predicted that south-facing nests would be subject to higher wind speeds, improving birds' ability to cool themselves evaporatively. Due to differences in evaporation, we expected south-facing nests would be less humid than east-facing nests. We explored interactions between temperature, humidity, and wind speed, in addition to temporal variation in the magnitude of differences, while accounting for potential deviations due to species-specific nest construction. We conducted our experiment over eight weeks during the 2019 breeding season (a non-drought year) by contrasting microclimates within pairs of unoccupied nests constructed by our two focal species placed in different orientations within the same microsite.

METHODS

We conducted the experiment at the Konza Prairie Biological Station (KPBS), a 3487-ha native tallgrass prairie located 15 km south of Manhattan, Kansas (Knapp et al. 1998). The KBPS is managed experimentally as part of the Long-Term Ecological Research program in units subject to multiple combinations of prescribed fire and grazing. The site has a mid-continental climate with mean daily temperatures in recent years of ~13 °C (Macpherson et al. 2008) and the mean maximum daily temperatures during July range from 29.4 °–35.6 °C (Craine et al. 2012). At KPBS, the sun rises 58.63 degrees from the north and sets 301.36 degrees from the north during peak summer, defined in this study as June–August (NOAA Solar Position Calculator, https://gml.noaa.gov/grad/solcalc/). Prevailing winds blow from south to north (Lysenko et al. 1994). There is high interannual variability in summer (May–September) precipitation with a 30-

yr rainfall average of 65.2 cm (CV of 29.8%; Knapp et al. 2015). During May–July 2019, a total of 52.9 cm of precipitation fell at KPBS; in 2018, a drought year, 20.5 cm of precipitation fell over the same time period (Nippert 2022).

Grasshopper Sparrows nest in grazed native prairies of moderate height, little-to-no wooded areas, and patchy bare ground mixed with clumps of vegetation (Shaffer et al. 2021). Eastern Meadowlarks build nests away from habitat edges and select somewhat taller, denser vegetation than Grasshopper Sparrows (Hubbard et al. 2006). Both species construct enclosed, domed nests from dead grasses on the ground (Roseberry and Klimstra 1970; Slater 2004), often placing nests beneath clumps of vegetation (i.e., *Amorpha canescens*, *Baptisia australis*, *Psoralidium tenuiflorum*, and *Andropogon gerardii*). In this experiment, we manipulated naturally constructed nests, as opposed to artificial nests, to approximate realistic conditions to the extent possible. Since neither species reuses nests, we carefully collected completed (i.e., fledged or failed) nests in 2017 and 2019 from both species. We dug and cut nests out of the surrounding vegetation using scissors and trowels, placing individual nests in small cardboard boxes, which we stored in plastic tubs until experimental initiation. We paired nests by mass, a subjective measure of light penetration, and general appearance to minimize differences in microclimate due to slight differences in nest construction.

We conducted the experiment from 12 June–3 August 2019, spanning the hottest and driest parts of the breeding season and capturing times when the thermoregulatory costs of overheating presumably peak at our site. We compared nest microclimate in eight experimental trials; each trial lasted four–six days. We compared microclimate in four–six nest pairs during each trial for a total of 18 Eastern Meadowlark and 16 Grasshopper Sparrow comparisons (n = 34). Distributing trials throughout the season allowed us to detect consequences of nest orientation associated with specific weather conditions and to explore the magnitude of microclimatic differences between differently oriented nests temporally.

We performed the experiment on a single, flat region of our study area to control for potential microclimate and habitat differences within the study site (Fig. 1). We placed 34 pairs of nests in suitable habitat along parallel ~50-m transects, spaced 10 m apart using a handheld GPS unit (GPSmap 60CSx; Garmin, Olathe, Kansas). At the start of each transect or 10-m mark, we selected and flagged the nearest plant species under which Eastern Meadowlarks and Grasshopper Sparrows commonly place nests. If there were no plants of those species within a meter of the point, we continued to a new point another 10 m northward. Under the selected plant, we parted the grass and fastened two similar conspecific nests to the ground with a nail, with the backs of the nests no more than six cm apart. Within each pair, the two nest cups faced a different direction based on the most common orientation from drought and non-drought years: east (90°; Grasshopper Sparrow) or northeast (45°; Eastern Meadowlarks) to represent typical years, and south (180°; both species) to represent the drought year orientation (Smith et al., in press).

Fig. 1. Diagram showing location of the Konza Prairie (A), location of study area within the site (B), and spatial arrangement of experimental nests (C–E). We conducted eight, four- to six-day trials over the course of the experiment. Each trial consisted of four to six pairs of conspecific nests (meadowlark or sparrow), with one pair placed every 10 meters along a transect line. Each pair was placed under the same plant, with pairs arrayed along parallel transect lines in subsequent trials.
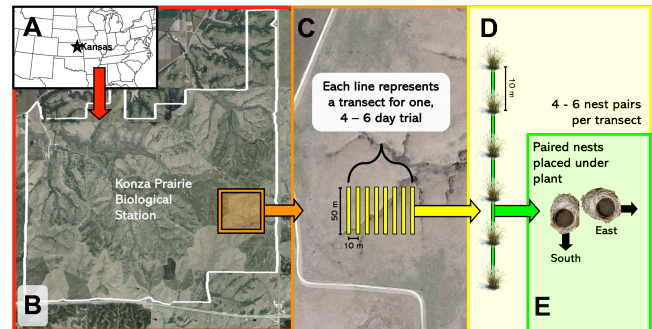
We assessed the consequences of orientation on microclimatic variation by measuring the temperature, humidity, and wind speed at each nest. We attached a small datalogger (DS1923-F5 # Hygrochron; iButton®) using Blu-Tack Reusable Adhesive (Bostic) to the underside of small plastic pizza savers and embedded the legs securely in the middle of each nest cup, suspending the dataloggers a couple of centimeters above the ground to measure conditions a nestling or parent would experience inside the nest. The shade from the pizza savers was unlikely to influence the recorded microclimate because the inside of these enclosed nests was already shaded from above. We programmed the dataloggers to record temperature (°C) and relative humidity (%RH) in 10-minute intervals throughout the day and night. We calculated mean hourly temperature and humidity values by averaging the six measurements per hour. We recorded wind speed (m/s) once per day, taking measurements during the hottest part of the day, between 10:00 and 13:00, using a handheld anemometer (Benetech, GM8908) at two locations relative to the nest: (1) immediately in front (at the height) of the nest entrance and facing the direction of the opening, parallel to the ground and perpendicular to the opening, and (2) a single set of measurements at 1 m above the nest pairs. We averaged eight measurements for each set of wind measurements, recorded every 10 seconds, to minimize the effects of gusts on mean wind speed comparisons.

Our response variables represented the differences between paired nests in temperature, humidity, and wind speed, calculated by subtracting the values of south-facing nests from their east-facing counterparts. We presented the difference values as opposed to the raw microclimatic variables to account for variation in the raw data unrelated to our experimental treatment. Thus, response variables reflect how birds mitigated expected costs that could occur if birds adopted standard orientations under drought conditions. Negative values indicated that south-facing nests were

warmer, more humid, or windier than east-facing nests, whereas positive values indicated that east-facing nests were warmer, more humid, or windier than south-facing nests.

We used an information theoretical approach to evaluate four sets of models explaining variation in the following response variables: differences between nest pairs in (1) temperature and (2) humidity, both measured from 09:00–17:00 which we anticipated would encompass peak daytime temperatures relevant to bird thermoregulation. To evaluate how humidity might modulate temperature differences, we again modeled (3) temperature differences, this time including raw humidity values measured in the south-facing nest as a covariate. We modeled differences in (4) wind speed, measured directly in front of nest cups. Because we only collected a single, midday set of wind measurements, we calculated mean differences in temperature and humidity between 11:00 and 13:00 to match the temporal resolution of the wind speed in analysis 4. Finally, we evaluated the consequence of wind speed (measured at 1 m above the nest pair) on temperature differences (5a) and humidity differences (5b) in the absence of temporal variables.

In all analyses, we included the fixed effect of the species that had constructed the nest to account for differences in overall size, opening size, and other elements of nest construction. We also included a random effect of nest pair to account for repeated measures. In analyses 1 and 2, we evaluated the fit of all models that accounted for temporal variation in the response variable combinations including the following factors: date, date², hour, hour², and date*hour. We included the polynomials to explore nonlinear diurnal or seasonal patterns in the data and the interaction term to account for changes in diurnal patterns as the season progressed. We did not include interactions involving the polynomial terms due to lack of a priori expectations of these more complex relationships and to enable interpretability of results. In analyses 3, we evaluated the fit of the same set of temporal variables to the temperature differences in combination with raw humidity from the south-facing nest. In the model selection procedure, we also evaluated the best-fit model from analysis 1 (temperature differences not including humidity) against all other models including humidity. In analyses 4, because we collected a single set of measurements per day, our temporal variables were restricted to date and date². Finally, because wind can influence both temperature and humidity, we analyzed associations between temperature differences (analysis 5a) and humidity differences (analysis 5b) with wind speed using the 145 raw wind speed values measured above the nest during the hottest part of the day (10:00–13:00), accounting for species and the random effect of nest pair as in above models.

We conducted all analyses using the lmer package (Bates et al. 2015) in R version 4.0.2 (R Core Development Team 2023). We compared competing models using Akaike's Information Criterion corrected for small sample size (AIC_c), considering parameters in competitive models where confidence intervals overlapped zero to be uninformative (Arnold 2010). We evaluated the correlations of variables in full model sets and assessed variance inflation factors for fixed effects, ensuring that it was less than five. We interpreted the model with the lowest AIC_c in each analysis. To evaluate overall differences between orientations, we assessed the sign (+/-) of the response variable and whether the

95% confidence intervals overlapped zero. We present the results of the AIC model selection for each of the analyses in Table 1 and present estimates of model coefficients from each of the top models in Table 2.

RESULTS

We collected 20,687 pairs of temperature and humidity measurements from 18 and 16 pairs of Eastern Meadowlark and Grasshopper Sparrow nests, respectively. Temperature differed between nests within pairs simultaneously by up to 23.5 °C. The difference in temperature between east- and south-facing nests varied strongly over the 24-hour period (Fig. 2A). Temperature differences were negligible from evening hours until about 07:00; however, east-facing nests warmed more quickly than south-facing nests, with temperature differences peaking at about 10:00, when east nests were, on average, 2.4 °C warmer than their south-facing counterparts. South-facing nests became warmer through the afternoon, with differences peaking at about 13:00, when east-facing nests were, on average, 3.7 °C cooler than their south-facing counterparts. Temporal patterns in humidity differences between nests were less clear; frequently, humidity differed little within pairs of differently oriented nests (Fig. 2B). Differences in humidity between pairs were as high as 56.8%, and peak differences occurred during the nighttime. Raw temperatures were lowest around 05:00–06:00 and peaked between 13:00–14:00, with raw nest temperatures ranging from 11.6°–59.0 °C (Fig. 2C). Raw humidity was less temporally predictable. Although humidity tended to decline somewhat in the middle of the day, it varied considerably throughout the 24-hour period, ranging from 10.5%–100% relative humidity (Fig. 2D). Based on meteorological data collected at the Konza headquarters in June–August 2019, mean daily air temperature was 24.3 °C, maximum air temperature was 36.4 °C, mean relative humidity was 68.1%, and maximum relative humidity was 99.1% (Nippert 2023; Fig. 2E and 2F).

Between 09:00–17:00, we recorded 1162 pairs of daytime temperature and humidity measurements. The comparison of models explaining variation in the temperature difference data (analysis 1) revealed that the model that best fit the data included species and hour² (see Table 1 for full AIC results of all analyses). This model accounted for 97% of model weight and was 7.97 AIC_c values lower than the next most competitive model. Daytime mean temperatures in south-facing nests were slightly warmer on average than east-facing nests (mean difference, −0.80 °C; 95% CI, −0.87 to −0.74 °C). The combination of temporal effects that best fit the humidity difference data (analysis 2) included the interaction between hour and date (Table 2). This model accounted for 59% of the AIC weight. One competing model was 1.49 ΔAIC_c lower than the top model and only differed in including hour²; that model accounted for 28% of AIC weight and was 3.50 ΔAIC_c higher than the next best model. During the daytime hours, east-facing nests were slightly more humid (0.85% RH; 95% CI, 0.54%–1.15%) relative to south-facing nests (Table 2). The effect of nest orientation on humidity changed throughout the day and throughout the season (Fig. 3); over the season, humidity shifted from being higher in east-facing nests to south-facing nests, and those declines were more pronounced in afternoon hours than morning hours. Analysis 3 revealed that raw humidity influenced temperature differences between east- and south-facing nests. As humidity increased, the temperature

Table 1. Full AICc tables from analyses 1–4. Response variables represent the difference due to orientation (i.e., between east- and south-facing nests) in microclimate.

Model set	Model terms*	logLik	AICc	AIC$_c$	K	weight
Analysis 1: Temperature differences						
	Species + hour + hour²	−3611.99	7236.05	0	6	0.97
	Species + date + hour + hour²	−3614.65	7243.38	7.32	7	0.03
	Species + date + hour + hour² + hour*date + (1|Nest_ID)	−3615.88	7247.88	11.83	8	2.60E-03
	Species + hour + hour² + date+ date² + (1|Nest_ID)	−3620.03	7256.18	20.13	8	4.15E-05
	Species + hour + hour² + date + date² + hour*date +(1|Nest_ID)	−3620.91	7259.95	23.90	9	6.29E-06
	Species + hour + (1|Nest_ID)	−3639.07	7288.19	52.13	5	4.65E-12
	Species + date + hour + (1|Nest_ID)	−3641.54	7295.14	59.08	6	1.44E-13
	Species + date + hour + hour*date + (1|Nest_ID)	−3642.43	7298.94	62.89	7	2.15E-14
	Species + date + date² + hour + (1|Nest_ID)	−3646.91	7307.91	71.85	7	2.43E-16
	Species + date + date² + hour + hour*date + (1|Nest_ID)	−3647.42	7310.95	74.89	8	5.31E-17
	Species + (1|Nest_ID)	−3772.70	7553.44	317.38	4	1.17E-69
	Species + date + (1|Nest_ID)	−3774.07	7558.18	322.12	5	1.10E-70
	Species + date + date² + (1|Nest_ID)	−3779.25	7570.57	334.52	6	2.23E-73
Analysis 2: Humidity differences						
	Species + date + hour + hour*date + (1|Nest_ID)	−5378.42	10770.93	0	7	0.59
	Species + date + hour + hour² + hour*date +(1|Nest_ID)	−5378.15	10772.42	1.49	8	0.28
	Species + date + hour + (1|Nest_ID)	−5381.93	10775.93	4.99	6	0.05
	Species + date + hour + hour² + (1|Nest_ID)	−5381.49	10777.07	6.13	7	0.03
	Species + date + date² + hour +hour*date + (1|Nest_ID)	−5380.77	10777.65	6.71	8	0.02
	Species + hour + hour² + date + date² + hour*date +(1|Nest_ID)	−5380.54	10779.22	8.28	9	9.50E-03
	Species + date + date² + hour + (1|Nest_ID)	−5382.57	10779.23	8.30	7	9.40E-03
	Species + hour + hour² + date + date² + (1|Nest_ID)	−5382.24	10780.60	9.66	8	4.70E-03
	Species + hour + (1|Nest_ID)	−5386.90	10783.85	12.92	5	9.30E-04
	Species + hour² + (1|Nest_ID)	−5386.06	10784.19	13.25	6	7.90E-04
	Species + date² + (1|Nest_ID)	−5424.88	10861.82	90.89	6	1.09E-20
	Species + date + (1|Nest_ID)	−5428.65	10867.34	96.40	5	6.93E-22
	Species + (1|Nest_ID)	−5439.08	10886.19	115.26	4	5.58E-26
Analysis 3: Temperature differences with humidity						
	Species + hour + hour² + humidity + (1|Nest_ID)	−3573.70	7161.49	0	7	0.94
	Species + ordinal + hour² + hour + humidity + (1|Nest_ID)	−3575.65	7167.41	5.92	8	0.05
	Species + hour + humidity + (1|Nest_ID)	−3579.78	7171.62	10.12	6	0.01
	Species + date + hour² + hour + humidity + hour*date + (1|Nest_ID)	−3577.33	7172.80	11.30	9	3.33E-03
	Species + date + hour +humidity + (1|Nest_ID)	−3581.39	7176.86	15.36	7	4.34E-04
	Species + hour + hour² + date + date² + humidity + (1|Nest_ID)	−3580.60	7179.33	17.84	9	1.26E-04
	Species + date + hour + hour*date + humidity + (1|Nest_ID)	−3582.96	7182.037	20.54	8	3.26E-05
	Species + date + hour² + date + hour + humidity + hour*date + (1|Nest_ID)	−3581.73	7183.64	22.14	10	1.46E-05
	Species + date + date² + hour + humidity + (1|Nest_ID)	−3586.24	7188.60	27.11	8	1.22E-06
	Species + date + date² + hour +hour*date + humidity+ (1|Nest_ID)	−3587.25	7192.63	31.14	9	1.63E-07
	Species +hour + hour² †	−3611.99	7236.05	74.56	6	6.08E-17
	Species + humidity + (1|Nest_ID)	−3667.07	7344.18	182.69	5	2.01E-40
	Species + date + humidity + (1|Nest_ID)	−3666.64	7345.34	183.84	6	1.13E-40
	Species + date + date² + humidity + (1|Nest_ID)	−3671.04	7356.17	194.68	7	5.02E-43
Analysis 4: Wind differences						
	Species + (1|Nest_ID)	58.1303825	−107.98	0	4	0.65
	Species + date + (1|Nest_ID)	58.1673716	−105.90	2.07	5	0.23
	Species + date + date² + (1|Nest_ID)	58.6273605	−104.65	3.33	6	0.12

† Top model from analysis 1.

differences shifted from being warmer in south-facing nests to being similar between nest pairs (mean temperature difference with humidity, 0.056 °C; 95% CI, 0.044 °–0.067 °C). Relative to analysis 1 models that included date, hour, and their interactions or the model that only included only raw humidity values in the south-facing nests, the model including both humidity and hour² provided the best fit to the data, accounting for 94% of the AIC weight (Table 1).

We collected 127 sets of wind speed measurements (one set per exposure day for each nest pair). Wind speeds varied from 0.26–5.59 m/s across the study period. In analysis 4, the model best

explaining the differences in wind speed at the nest cup level between pairs included only species and the random effect of nest pair ID, which was essentially our null model. Neither a linear nor quadratic term for date explained much variation in this dataset, with one model being 2.07 ΔAIC$_c$ below the top model and the other being 3.33 ΔAIC$_c$ below the top model.

The top wind model revealed that wind speeds at domed nest entrances were higher at the entrances of south-facing nests than east-facing nests (mean difference in wind speed predicted values, −0.03 m/s; 95% CI, −0.033 to −0.029). However, the magnitude of this difference (only 0.03 m/s) may mean that, biologically, such

Table 2. Parameter estimates from top models in analyses 1–5. Response variables represent the difference in an environmental variable between nests (i.e., east–south). Bold font indicates variables with confidence intervals not overlapping 0. In comparisons of species effects, values from Eastern Meadowlark (*Sturnella magna*) nests represent the reference level and beta estimates reflect differences in Grasshopper Sparrow (*Ammodramus savannarum*) nests.

Model	Variable	Beta estimate	Lower 95% CI	Upper 95% CI	Variance ± SD
Model 1: Temperature differences					
	Intercept	**31.33**	**25.45**	**37.22**	
	Hour	**−4.42**	**−5.35**	**−3.50**	
	Hour²	**0.14**	**0.11**	**0.18**	
	Species	0.73	−0.39	1.85	
	Random: NestID				2.36 ± 1.54
	Residual				14.52 ± 3.81
Model 2: Humidity differences					
	Intercept	**182.77**	**93.08**	**266.86**	
	Date	**−1.07**	**−1.51**	**−0.61**	
	Hour	**−6.27**	**−10.36**	**−2.16**	
	Date*hour	**0.04**	**0.02**	**0.06**	
	Species	4.00	−4.56	12.63	
	Random: NestID				164.80 ± 12.84
	Residual				214.60 ± 14.65
Model 3: Temperature differences with humidity					
	Intercept	**16.37**	**9.89**	**22.89**	
	South-facing nest humidity	**0.06**	**0.044**	**0.07**	
	Hour	**−2.68**	**−3.65**	**−1.72**	
	Hour²	**0.08**	**0.044**	**0.12**	
	Species	0.74	−0.37	1.86	
	Random: NestID				2.36 ± 1.54
	Residual				13.59 ± 3.69
Model 4: Wind differences					
	Intercept	**−0.04**	**−0.08**	**−2.0E-3**	
	Species	0.02	−0.04	0.08	
	Random: NestID				6.80E-04 ± 0.03
	Residual				0.03 ± 0.16
Model 5a: Temperature differences					
	Intercept	−0.46	−1.69	0.74	
	Wind speed	−0.17	−0.67	0.32	
	Species	0.60	−0.60	1.83	
	Random: NestID				0.30 ± 0.55
	Residual				11.41 ± 3.38
Model 5b: Humidity differences					
	Intercept	−4.17	−10.53	2.21	
	Wind speed	1.53	−0.42	3.49	
	Species	2.54	−5.12	10.18	
	Random: NestID				80.47 ± 8.97
	Residual				164.94 ± 12.84

differences are inconsequential. Analyses of temperature (5a) and humidity (5b) differences that incorporated wind speed at 1 m above the nest revealed that wind speed above the nest did not influence the effect of nest orientation on temperature (mean difference in temperature from wind, −0.17 °C; 95% CI, −0.67 to 0.32) or humidity (mean difference in humidity from wind, 1.53%; 95% CI, −0.42 to 3.49). We did not find evidence that orientation influenced any aspect of microclimate differently in nests constructed by Grasshopper Sparrows or Eastern Meadowlarks because the 95% CI surrounding the beta estimate for species in all models overlaps 0 (Table 2).

DISCUSSION

In an experimental manipulation of the orientation of ground-nesting, grassland-dependent bird nests, we demonstrated that the direction of nest openings does indeed influence nest microclimate. Independent of nest micro-site and species-level differences in nest architecture, the nonrandom orientation of nests influences the temperatures inside the nest. However, the ways that temperature differs in domed nests with a standard orientation (i.e., generally facing approximately east) relative to the orientations many birds selected during a dry and hot drought year (i.e., generally facing south) were more complex than we predicted. The south-facing nests were not consistently cooler over the whole 24-hour period nor during all daylight hours. Rather, orientation affected the timing of nest warming in combination with humidity. As predicted, south-facing nests warmed more slowly in the morning than east-facing nests. Temperature differences within pairs of nests were greatest when humidity was low, but there were no overall temperature differences. Although wind speed was higher at the openings of south-facing nests, this difference was very small, and wind did not appear to influence temperature or humidity differences.

The similarity between microclimatic measurements from our two focal species suggests that orientation likely has an adaptive function in this system, as in some other birds (Briggs and Mainwaring 2021; but also see Lloyd and Martin 2004). The nature of responses provides insight into the potential benefits of behavioral choices. In a hot, dry year, overall humidity is lower, meaning that the conditions we measured when humidity was low may better approximate those experienced by incubating and brooding females during droughts. Our results suggest that slowing early morning warming may be a key consideration. Slowing early morning warming may be beneficial in an unseasonably hot drought year because ambient temperature warms more quickly under low humidity, and this period of slow warming may provide a buffer that prevents heat stress during the hours with the coolest temperature during a non-drought year. The delay in warming may function in the context of extending cooler nighttime temperatures for longer periods during hot summer days. However, behavioral plasticity can only mitigate adverse conditions up to a point. Whereas shifts in orientation reduced the morning warming rate, they resulted in more extreme, higher mid-afternoon temperatures than the east-facing nests.

We did not find an effect of orientation on the wind speed measured at the nest entrance nor evidence that wind speed influenced the differences in temperature and humidity between nest pairs. However, we only collected wind speed once daily, and more frequent or precise measures may have revealed associations between these microclimatic factors. At the same time, the biological effects of wind may not be realistically measured by dry-bulb temperatures as we did in this study (James 1970). Birds use evaporation to cool themselves during hot spells, and evaporation occurs more effectively under higher wind speeds (McKechnie and Wolf 2019). Thus, our conclusions regarding the lack of wind in influencing nest microclimate must be interpreted with caution due to the limitations of our dataset.
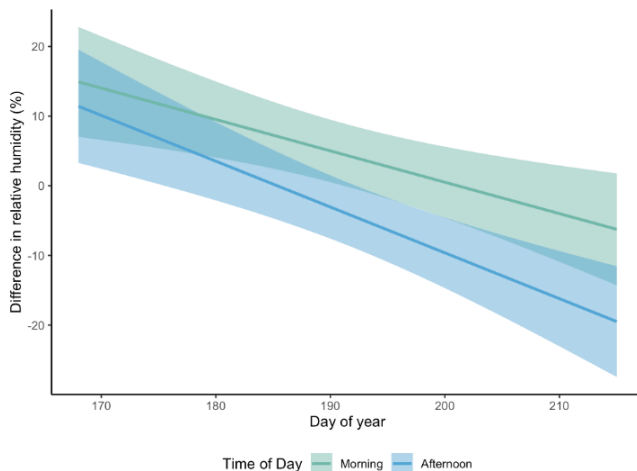
There are few experimental studies of nest orientation (Ricklefs and Hainsworth 1969; Butler et al. 2009; Landler et al. 2014), most of which are from cavity-nesting species. This is unsurprising

Fig. 2. Differences in temperature (panel A) and % relative humidity (panel B) between east- and south-facing nests over 24 h throughout the study. Positive values on *y*-axes indicate higher temperature or humidity values in east-facing nests, which reflect typical nest orientations, whereas negative values on the *y*-axis indicate higher values in south-facing nests, an orientation common during drought. Data from Eastern Meadowlark (*Sturnella magna*) nests are plotted in gold, and Grasshopper Sparrow (*Ammodramus savannarum*) nests are plotted in brown. Panels C and D depict raw nest temperatures and % humidity, respectively, with east-facing nests in dark blue and south-facing nests in light blue. Panels E and F depict ambient air temperature and relative humidity, respectively, obtained from the Konza Prairie LTER weather station (Nippert 2023).
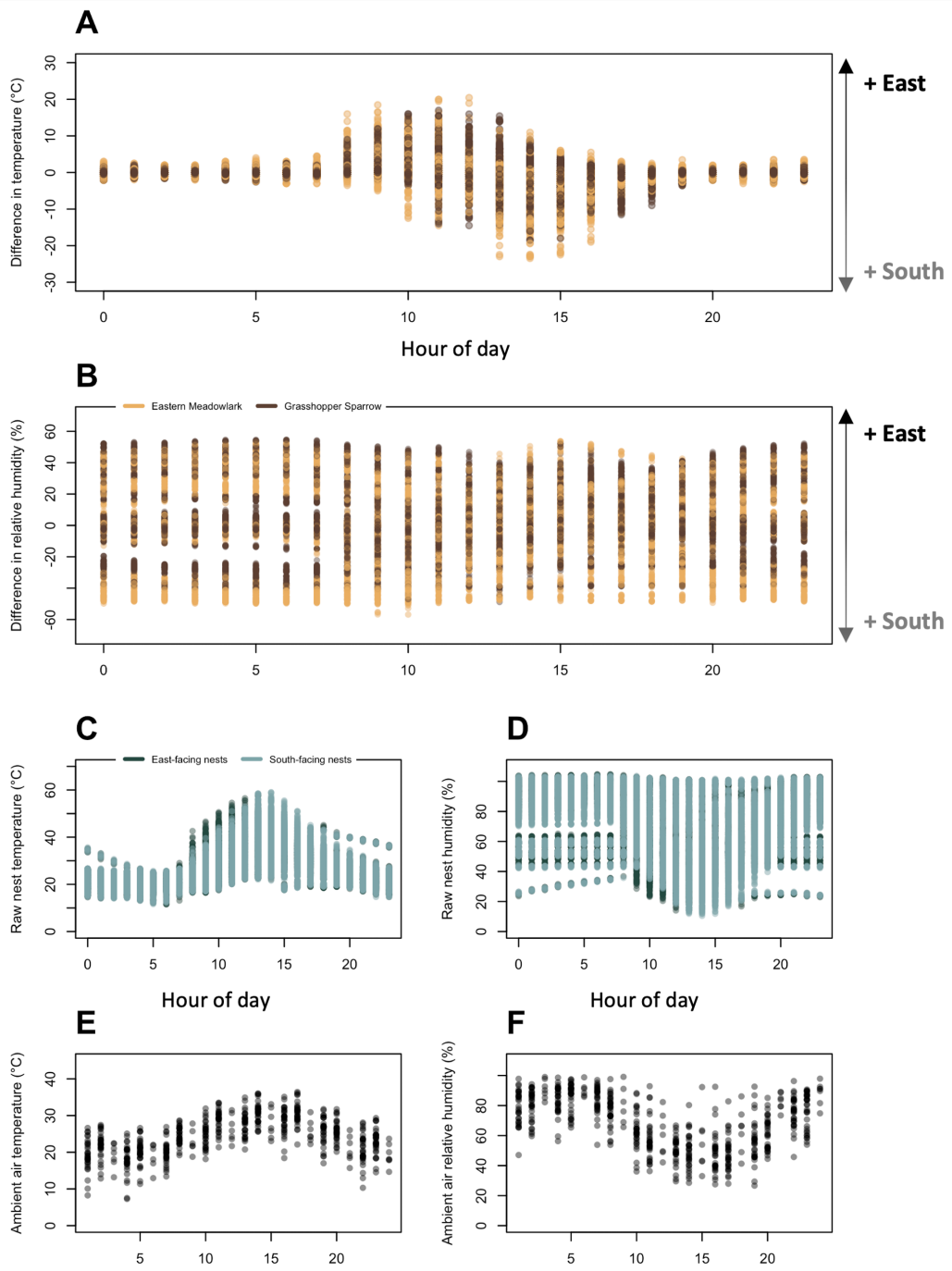
Fig. 3. Seasonal humidity differences between east- and south-facing nests from the top model in analysis 2. Positive values indicate drier conditions inside the east-facing (control) nests. We modeled time continuously but visualized the interaction between time and date by dividing daylight hours into morning and afternoon periods. The green line (and shaded Wald confidence intervals) indicate nests measured during morning hours (09:00–11:59), and the blue line and shading correspond to measurements taken during the afternoons (12:00–17:00).

data imply that ground-nesting birds may be able to behaviorally mitigate such conditions, at least up to a certain point (Wuebbles et al. 2017). However, our data also show that the ability to modulate microclimate through nest orientation has limits. Although the future is bleak for grassland-dependent birds, (Rosenberg et al. 2019) adaptive plasticity in nest orientation is potentially one of several strategies birds can employ to cope with climatic stressors.

Data Availability:

The dataset associated with this paper is openly available in Dryad at https://doi.org/10.5061/dryad.crjdfn37f.

due to these species' readiness to occupy artificial cavities, which are an easy medium for orientation manipulation (Landler et al. 2022). However, restricting experimental studies of nest orientation and microclimate to one nest type fails to account for the very narrowly constrained microclimates (35 °–37 °C) that are suitable for embryonic and nestling development relative to the broad range of weather conditions that nesting birds face. Bramblings (*Fringilla montifringilla*), for example, frequently nesting in the snow (Zabala et al. 2012), will experience vastly different fitness benefits of warming and cooling than arid-land birds where air temperatures often exceed 40 °C (Ruth and Skagen 2017). The consequences of changing climatic conditions will likely influence fitness differently depending on the how close a population is to factors limiting its distribution (Boyle et al. 2020). Thus, local shifts in orientation ought to be interpreted in the context of the local environment, and inferences should take into account factors such as nest placement (Hernández and Zaldívar 2021) and architecture (Souza and Santos 2007; Greeney 2008).

Due to widespread associations between fledging success and orientation in directional nests, there is a strong potential for behavioral plasticity in orientation during nest building to influence fitness (Verbeek 1981; Lloyd and Martin 2004; Landler et al. 2022). Such plasticity is good news for birds coping with reproduction under variable climatic conditions such as those experienced in the Great Plains of North America and elsewhere (Knapp and Smith 2015). However, grassland birds are already a highly threatened guild, partly due to human-caused climate change (Skagen and Adams 2012; Jarzyna et al. 2016) that is anticipated to increase the incidence of drought and hot periods during temperate summers (Brookshire and Weaver 2015). These

LITERATURE CITED

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175-1178. https://doi.org/10.2193/2009-367

Bates, D., M. Mächler, B. M. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1-48. https://doi.org/10.48550/arXiv.1406.5823

Boyle, W. A., E. H. Shogren, and J. D. Brawn. 2020. Hygric niches for tropical endotherms. Trends in Ecology and Evolution 35: 938-952. https://doi.org/10.1016/j.tree.2020.06.011

Briggs, K. B., and M. C. Mainwaring. 2021. The orientation of nestboxes influences their occupation rates and the breeding success of passerine birds. Ornis Hungarica 29:107-121. https://doi.org/10.2478/orhu-2021-0023

Brookshire, E. N. J., and T. Weaver. 2015. Long-term decline in grassland productivity driven by increasing dryness. Nature Communications 6:7148. https://doi.org/10.1038/ncomms8148

Burnette, D. J., D. W. Stahle, and C. J. Mock. 2010. Daily-mean temperature reconstructed for Kansas from early instrumental and modern observations. Journal of Climate 23:1308-1333. https://doi.org/10.1175/2009JCLI2445.1

Burton, N. H. K. 2006. Nest orientation and hatching success in the tree pipit *Anthus trivialis*. Journal of Avian Biology 37:312-317. https://doi.org/10.1111/j.2006.0908-8857.03822.x

Burton, N. H. K. 2007. Intraspecific latitudinal variation in nest orientation among ground-nesting passerines: a study using published data. Condor 109:441-446. https://doi.org/10.1093/condor/109.2.441

Butler, M. W., B. A. Whitman, and A. M. Dufty. 2009. Nest box temperature and hatching success of American Kestrels varies with nest box orientation. Wilson Journal of Ornithology 121:778-782. https://doi.org/10.1676/08-124.1

Carroll, J. M., C. A. Davis, R. D. Elmore, and S. D. Fuhlendorf. 2015. A ground-nesting galliform's response to thermal heterogeneity: implications for ground-dwelling birds. PLoS ONE 10(11):e0143676. https://doi.org/10.1371/journal.pone.0143676

Charter, M., K. Meyrom, Y. Leshem, S. Aviel, I. Izhaki, and Y. Motro. 2010. Does nest box location and orientation affect occupation rate and breeding success of Barn Owls (*Tyto alba*) in a semi-arid environment? Acta Ornithologica 45:115-119. https://doi.org/10.3161/000164510X516164

Collias, N. E. 1997. On the origin and evolution of nest building by passerine birds. Condor 99:253-270. https://doi.org/10.2307/1369932

Craine, J. M., J. B. Nippert, A. J. Elmore, A. M. Skibbe, S. L. Hutchinson, and N. A. Brunsell. 2012. Timing of climate variability and grassland productivity. Proceedings of the National Academy of Sciences of the United States of America 109:3401-3405. https://doi.org/10.1073/pnas.1118438109

DuRant, S. E., W. A. Hopkins, G. R. Hepp, and J. R. Walters. 2013. Ecological, evolutionary, and conservation implications of incubation temperature-dependent phenotypes in birds. Biological Reviews 88:499-509. https://doi.org/10.1111/brv.12015

Duursma, D., R. Gallagher, J. Price, and S. Griffith. 2018. Variation in avian egg shape and nest structure is explained by climatic conditions. Scientific Reports 8:4141. https://doi.org/10.1038/s41598-018-22436-0

Edwards, S. C., T. T. Shoot, R. J. Martin, D. F. Sherry, and S. D. Healy. 2020. It's not all about temperature: breeding success also affects nest design. Behavioral Ecology 31:1065-1072. https://doi.org/10.1093/beheco/araa052

Fulton, G. R. 2019. Meta-analyses of nest predation in temperate Australian forests and woodlands. Austral Ecology 44:389-396. https://doi.org/10.1111/aec.12698

Goodenough, A. E., D. P. Maitland, A. G. Hart, and S. L. Elliot. 2008. Nestbox orientation: a species-specific influence on occupation and breeding success in woodland passerines. Bird Study 55:222-232. https://doi.org/10.1080/00063650809461526

Greeney, H. F. 2008. Nest construction behavior and variability in nest architecture and nest placement of the Spotted Barbtail (*Premnoplex brunnescens*). Boletín SAO 18:26-37. https://www.researchgate.net/publication/228917410_Nest_construction_behavior_and_variability_in_nest_architecture_and_nest_placement_of_the_Spotted_Barbtail_Premnoplex_brunnescens

Hartman, C. A., and L. W. Oring. 2003. Orientation and microclimate of Horned Lark nests: the importance of shade. Condor 105:158-163. https://doi.org/10.1093/condor/105.1.158

Hernández, Á., and P. Zaldívar. 2021. Nest-site selection and nest design of Iberian bullfinches *Pyrrhula pyrrhula iberiae* in northwestern Spain. Avian Biology Research 14:124-142. https://doi.org/10.1177/17581559211037501

Hubbard, R. D., D. P. Althoff, K. A. Blecha, B. A. Bruvold, and R. D. Japuntich. 2006. Nest site characteristics of eastern meadowlarks and grasshopper sparrows in tallgrass prairie at the Fort Riley military installation, Kansas. Transactions of the Kansas Academy of Science 109:168-174. https://www.jstor.org/stable/20476268

Ingels, J., J. H. Ribot, and B. H. J. De Jong. 1984. Vulnerability of eggs and young of the Blackish Nightjar (*Caprimulgus nigrescens*) in Suriname. Auk 101:388-391. https://doi.org/10.1093/auk/101.2.425

James, F. C. 1970. Geographic size variation in birds and its relationship to climate. Ecology 51:365-390. https://doi.org/10.2307/1935374

Jarzyna, M. A., B. Zuckerberg, A. O. Finley, and W. F. Porter. 2016. Synergistic effects of climate and land cover: grassland birds are more vulnerable to climate change. Landscape Ecology 31:2275-2290. https://doi.org/10.1007/s10980-016-0399-1

Kim, S. Y., and P. Monaghan. 2005. Effects of vegetation on nest microclimate and breeding performance of lesser black-backed gulls (*Larus fuscus*). Journal of Ornithology 146:176-183. https://doi.org/10.1007/s10336-005-0077-6

Knapp, A., J. Briggs, D. Harnett, and S. Collins. 1998. Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York, New York, USA.

Knapp, A. K., C. J. W. Carroll, E. M. Denton, K. J. La Pierre, S. L. Collins, and M. D. Smith. 2015. Differential sensitivity to regional-scale drought in six central US grasslands. Oecologia 177:949-957. https://doi.org/10.1007/s00442-015-3233-6

Knapp, A. K., and M. D. Smith. 2015. Variation among biomes in temporal dynamics of aboveground primary production. Science 291:481-484. https://doi.org/10.1126/science.291.5503.481

Landler, L., M. A. Jusino, J. Skeleton, and J. R. Walters. 2014. Global trends in woodpecker cavity entrance orientation: latitudinal and continental effects suggest regional climate influence. Acta Ornithologica 49:257-266. https://doi.org/10.3161/173484714X687145

Landler, L., J. Skeleton, M. A. Jusino, A. Van Lanen, and J. R. Walters. 2022. Effects of cavity orientation on nesting success inferred from long-term monitoring of the endangered red-cockaded Woodpecker. Scientific Reports 12:11624. https://doi.org/10.1038/s41598-022-15201-x

Lloyd, J. D., and T. E. Martin. 2004. Nest-site preference and maternal effects on offspring growth. Behavioral Ecology 15:816-823. https://doi.org/10.1093/beheco/arh085

Long, A. M., W. E. Jensen, and K. A. With. 2009. Orientation of Grasshopper Sparrow and Eastern Meadowlark nests in relation to wind direction. Condor 111:395-399. https://doi.org/10.1525/cond.2009.080076

Lysenko, I. A., Yu. I. Portnyagin, A. N. Fakhrutdinova, R. A. Ishmuratov, A. H. Manson, and C. E. Meek. 1994. Wind regime at 80–110 km at mid-latitudes of the northern hemisphere. Journal of Atmospheric and Terrestrial Physics 56:31-42. https://doi.org/10.1016/0021-9169(94)90173-2

Macpherson, G. L., J. A. Roberts, J. M. Blair, M. A. Townsend, D. A. Fowle, and K. R. Beisner. 2008. Increasing shallow groundwater CO2 and limestone weathering, Konza Prairie, USA. Geochimica et Cosmochimica Acta 72:5581-5599. https://doi.org/10.1016/j.gca.2008.09.004

Mainwaring, M. C., I. R. Hartley, M. M. Lambrechts, and D. C. Deeming. 2014. The design and function of birds' nests. Ecology and Evolution 4:3909-3928. https://doi.org/10.1002/ece3.1054

Martin, T. E., A. J. Boyce, K. Fierro-Calderòn, A. E. Mitchell, C. E. Armstad, J. C. Mouton, and E. E. Bin Soudi. 2017. Enclosed nests may provide greater thermal than nest predation benefits compared with open nests across latitudes. Functional Ecology 31:1231-1240. https://doi.org/10.1111/1365-2435.12819

Matysioková, B., and V. Remeš. 2018. Evolution of parental activity at the nest is shaped by the risk of nest predation and ambient temperature across bird species. Evolution 72:2214-2224. https://doi.org/10.1111/evo.13580

McKechnie, A. E., and B. O. Wolf. 2019. The physiology of heat tolerance in small endotherms. Physiology 34:302-313. https://doi.org/10.1152/physiol.00011.2019

Mishra, V., K. A. Cherkauer, and S. Shukla. 2010. Assessment of drought due to historic climate variability and projected future climate change in the midwestern United States. Journal of Hydrometeorology 11:46-68. https://doi.org/10.1175/2009JHM1156.1

Nippert, J. 2022. APT01 daily precipitation amounts measured at multiple sites across konza prairie. Environmental Data Initiative. http://doi.org/10.6073/pasta/434ea64024920232e8260f42f00c3fb6

Nippert, J. 2023. AWE01 Meteorological data from the konza prairie headquarters weather station. Environmental Data Initiative. http://doi.org/10.6073/pasta/743c6b205e38a087bc549-25ed258f549

Perez, D. M., J. L. Gardner, and I. Medina. 2020. Climate as an evolutionary driver of nest morphology in birds: a review. Frontiers in Ecology and Evolution 8:566018. https://doi.org/10.3389/fevo.2020.566018

R Core Team. 2023. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org

Rahmani, V., S. L. Hutchinson, J. A. Harrington, J. M. S. Hutchinson, and A. Anandhi. 2015. Analysis of temporal and spatial distribution and change-points for annual precipitation in Kansas, USA. International Journal of Climatology 35:3879-3887. https://doi.org/10.1002/joc.4252

Ricklefs, R. E., and F. R. Hainsworth. 1969. Temperature regulation in nestling Cactus Wrens: the nest environment. Condor 71:32-37. https://doi.org/10.2307/1366045

Roseberry, J. L., and W. D. Kimstra. 1970. The nesting ecology and reproductive performance of the Eastern Meadowlark. Wilson Bulletin 82(3):243-267. https://www.jstor.org/stable/4159977

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, and P. P Marra. 2019. Decline of the North American avifauna. Science 366:120-124. https://doi.org/10.1126/science.aaw1313

Ruth, J. M., and S. K. Skagen. 2017. Territory and nest site selection patterns by Grasshopper Sparrows in southeastern Arizona. Condor 119:469-483. https://doi.org/10.1650/CONDOR-16-210.1

Schaaf, A. A., and M. R. de la Peña. 2020. Bird nest orientation and local temperature: an analysis over three decades. Ecology 101:e03042. https://doi.org/10.1002/ecy.3042

Schaaf, A. A., C. G. García, P. B. Puechagut, L. E. Silvetti, E. Tallei, F. Ortis, and A. I. E. Quaglia. 2018. Effect of geographical latitude and sun exposure on Rufous Hornero (*Furnarius rufus*) nest orientation. Journal of Ornithology 159:967-974. https://doi.org/10.1007/s10336-018-1569-5

Shaffer, J. A., L. D. Igl, D. H. Johnson, M. L. Sondreal, C. M. Goldade, M. P. Nenneman, T. L. Wooten, and B. R. Euliss. 2021. The effects of management practices on grassland birds—Grasshopper Sparrow (*Ammodramus savannarum*). Pages 1842-1857 in D. H. Johnson, L. D. Igl, J. A. Shaffer, and J. P. DeLong, editors. The effects of management practices on grassland birds: U.S. Geological Survey Professional Paper 1842. https://doi.org/10.3133/pp1842GG

Skagen, S. K., and A. A. Y. Adams. 2012. Weather effects on avian breeding performance and implications of climate change. Ecological Applications 22:1131-1145. https://doi.org/10.1890/11-0291.1

Slater, G. L. 2004. Grasshopper Sparrow (*Ammodramus savannarum*): A technical conservation assessment peer review administered by society for conservation biology. US Forest Service, Rocky Mountain Region, Mount Vernon, Washington, USA.

Smith, E. B., A. J. Roe, K. M. Silber, E. J. Williams, S. K. Winnicki, and W. A. Boyle. In press. Consequences of drought for grassland songbird reproduction. Ecosphere.

Souza, F. L., and C. A. Santos. 2007. Climate and nest opening orientation in Furnarius rufus (Furnariidae). Iheringia. Série Zoologia 97:293-295. https://doi.org/10.1590/S0073-47212007000300013

Sugita, M., and W. Brutsaert. 1990. Wind velocity measurements in the neutral boundary layer above hilly prairie. Journal of Geophysical Research 95:7617-7624. https://doi.org/10.1029/JD095iD06p07617

Sutter, G. C. 1997. Nest-site selection and nest-entrance orientation in Sprague's Pipit. Wilson Bulletin 109:462-469. https://www.jstor.org/stable/4163841

Tulp, I., H. Schekkerman, and J. de Leeuw. 2012. Eggs in the freezer: energetic consequences of nest site and nest design in arctic breeding shorebirds. PLoS ONE 7:e38041. https://doi.org/10.1371/journal.pone.0038041

Verbeek, N. A. M. 1981. Nesting success and orientation of Water Pipit Anthus spinoletta nests. Ornis Scandinavica 12:37-39. https://doi.org/10.2307/3675902

Webb, D. R., and J. R. King. 1983. An analysis of the heat budgets of the eggs and nest of the white-crowned sparrow, Zonotrichia leucophrys, in relation to parental attentiveness. Physiological Zoology 56:493-505. https://doi.org/10.1086/physzool.56.4.30155872

White, F. N., and J. L. Kinney. 1974. Avian incubation: interactions among behavior, environment, nest, and eggs result in regulation of egg temperature. Science 186:107-115. https://doi.org/10.1126/science.186.4159.107

With, K. A., and D. R. Webb. 1993. Microclimate of ground nests: the relative importance of radiative cover and wind breaks for three grassland species. Condor 95:401-413. https://doi.org/10.2307/1369363

Wuebbles, D. J., D. W. Fahey, K. A. Hibbard, D. J. Dokken, B. C. Stewart, and T. K Maycock, editors. 2017. Climate science special report: Fourth National Climate Assessment. U.S. Global Change Research Program, Washington, DC, USA. https://science2017.globalchange.gov/

Zabala, J., I. Zuberogoitia, G. Belamendia, and J. Arizaga. 2012. Micro-habitat use by bramblings *Fringilla montifringilla* within a winter roosting site: influence of microclimate and human disturbance. Acta Ornithologica 47:179-184. https://doi.org/10.3161/000164512X662287