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ORIENTATION OF GRASSHOPPER SPARROW AND EASTERN MEADOWLARK NESTS IN RELATION TO WIND DIRECTION

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Abstract. Orientation of the entrances of bird nests may be especially important in grasslands, where protective cover from solar radiation and wind is minimal. We examined orientation patterns of nest-dome entrances in two grassland bird species, the Grasshopper Sparrow (*Ammodramus savannarum*) and the Eastern Meadowlark (*Sturnella magna*). We noted how these patterns changed over the nesting season and how they related to prevailing wind direction. We found that Grasshopper Sparrow ($n = 333$) and Eastern Meadowlark ($n = 272$) nests were oriented nonrandomly, toward the northeast ($\bar{a} = 33.4°$ and 52.9°, respectively). Prevailing wind in the study region was approximately from the south ($\bar{a} = 171.1°$); therefore, nests of the two species were generally oriented downwind. Nest orientation of the Eastern Meadowlark shifted northward as the nesting season progressed, coinciding with a southeastward shift in prevailing wind direction. Conversely, in one year we observed a seasonal shift toward the east in nest orientation of the Grasshopper Sparrow. Nest orientation in these species may represent a trade-off between various factors, including wind and solar radiation.

Key words: Ammodramus savannarum, *dome-shaped nests, grassland birds, nest orientation, nest-site selection,* Sturnella magna.

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Orientación de los Nidos de *Ammodramus savannarum* y *Sturnella magna* con Relación a la Dirección del Viento

Resumen. La orientación que eligen las aves para las entradas de los nidos puede ser especialmente importante en los pastizales, donde la cobertura que protege de la radiación solar y del viento es limitada. Examinamos los patrones de orientación de las entradas de los nidos con forma de domo de dos especies de aves de pastizal, *Ammodramus savannarum* y *Sturnella magna*, y evaluamos cómo estos patrones cambian a lo largo de la estación reproductiva y cómo se relacionan con la dirección predominante del viento. Encontramos que los nidos de *A. savannarum* (n = 333) y de *S. magna* (n = 272) presentaron orientaciones no azarosas hacia el noreste ($\bar{a}$ = 33.4° y 52.9°, respectivamente). El viento predominante en el área de estudio fue aproximadamente desde el sur ($\bar{a}$ = 171.1°); por ende, los nidos de las dos especies estuvieron generalmente orientados en dirección contraria al viento. La orientación del nido en *S. magna* varió hacia el norte a medida que la estación de anidación avanzó, lo que coincidió con un cambio hacia el sudeste en la dirección predominante del viento. Por el contrario, en un año observamos un cambio estacional en la orientación del nido hacia el este en *A. savannarum*. La orientación del nido en estas especies puede representar un balance de costo–beneficio entre varios factores, incluyendo el viento y la radiación solar.

Orientation of bird nests is often nonrandom with respect to nest-site vegetation (e.g., Hoekman et al. 2002), tree boles (for cavity nests; e.g., Wiebe 2001), and topography (e.g., Van Horn and Donovan 1994). A nest's orientaton can affect its exposure and thus its microclimate (Walsberg 1981, With and Webb 1993, Wiebe 2001, Hoekman et al. 2002, Rauter et al. 2002, Burton 2007), which in turn may affect egg and nestling survival (Austin 1974, Webb 1987, Rauter et al. 2002, Burton 2006) or confer thermoregulatory benefits to incubating or brooding adults (With and Webb 1993). Shifts in nest orientation over the nesting season may reflect responses of nesting birds to changing microclimates (Austin 1974, Hoekman et al. 2002). In general, latitudinal variation in nest orientation is consistent with the expectation that birds either orient nests toward or seek shelter from solar radiation (Burton 2007).

Amelioration of climatic stressors via nest orientation may be especially important for birds nesting in grasslands (With and Webb 1993, Hoekman et al. 2002, Hartman and Oring 2003), where there is little vegetative cover. In open grasslands, the directionality of nest orientation relative to surrounding vegetation has been shown to influence solar conductance and convective cooling at the nest (With and Webb 1993, Hartman and Oring 2003, Lloyd and Martin 2004). Several birds that nest in grasslands build dome-shaped nests with a canopy of grasses that partially or completely cover the nest cup (e.g., Northern Bobwhite, *Colinus virginianus*, Brennan 1999; Grasshopper Sparrow, *Ammodramus savannarum*, Vickery 1996; meadowlarks, *Sturnella* spp., Lanyon 1995). The lateral entrance of these nests exposes incubating adults and nest contents to the ambient environment and in some species appears to have a directional bias (Lanyon 1957, Roseberry and Klimstra 1970, Vickery 1996).

We explored patterns of nest orientation in two grassland bird species that build dome-shaped nests, the Grasshopper Sparrow and Eastern Meadowlark (*S. magna*), in the tallgrass prairie of eastern Kansas and Oklahoma. Amelioration of climatic factors, such as wind, might be an important consideration for nest placement in open grasslands; therefore, we predicted that in these species nest-dome orientation would be nonrandom and directed away from prevailing winds. Furthermore, we expected that any seasonal shifts in nest orientation would be coincident with a seasonal shift in prevailing wind direction.

METHODS

STUDY AREA

Our study was conducted on private and public lands, 51 sites total, located throughout the Flint Hills region of Kansas and Oklahoma (38° N, 96° W) during the breeding seasons (May–July) of 2004 and 2005. Air temperature and wind speed ranged from −2.3 to 38.3 °C and 0.4 to 10.3 m sec^{-1}, respectively, during the period of investigation (Konza Prairie Biological Station, http://www.konza.ksu.edu/data_catalog/toc.html, accessed 16 January 2009). The characteristic vegetation of the Flint Hills is tallgrass prairie dominated by grasses such as big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), Indian grass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*) (Freeman 1998). Other vegetation includes forbs such as lead plant (*Amorpha canescens*), smooth sumac (*Rhus glabra*), and buckbrush (*Symphoricarpos orbiculatus*) (Abrams et al. 1986, Freeman 1998). The study sites were representative of the predominant grassland-management practices of the region, which include prescribed burning, various cattle-grazing systems, mowing for hay, and grasslands restored through the U.S. Department of Agriculture's Conservation Reserve Program. For more details regarding the study sites, refer to With et al. (2008).

NEST AND WIND DATA

We searched for nests by a combination of methods, including the observation of adults, rope dragging, and haphazard flushing of incubating females, from early May through the end of July. Nests were marked with blue wire flags 5 m away and relocated by the global-positioning system. We monitored nests as part of a larger project investigating land-management effects on grassland birds (Frey et al. 2008, With et al. 2008, Rahmig et al. 2009). We measured the orientation of dome entrances of Grasshopper Sparrow and Eastern Meadowlark nests (relative to magnetic north) as a compass bearing (0–359°) at the conclusion of each nesting attempt. We rarely observed nest initiation, so we estimated the date of initiation by backdating from known laying or hatching dates or as the midpoint between minimum and maximum possible nest-initiation dates for nests in which we observed only eggs prior to depredation. We based our estimates of the duration of nest construction and incubation on Lanyon (1995) and Baicich and Harrison (1997).

Detailed hourly weather data, including wind speed (m sec^{-1}) and direction, were available from the weather station at the Konza Prairie Biological Station in the northern Flint Hills (39° 05′ N, 96° 35′ W) (http://www.konza.ksu.edu/data_catalog/toc.html, accessed 16 January 2009). We used wind data from 1 May to 31 July, 2004 and 2005, which encompassed the majority of the nesting season of our study species. We consider these data representative of conditions across our study region. We estimated prevailing wind direction as the mean across all hourly observations and years. Wind direction did not differ significantly (Watson–Williams two-sample test: $F_{1, 4414}$ = 3.0, P = 0.1) between day (06:00−21:00) ($\bar{a}$ = 173.4°, s = 55.5°) and night ($\bar{a}$ = 167.8°, s = 42.8°). To evaluate seasonal shifts in wind direction, we used daily measurements at 15:00, when mean wind speed was at its maximum (4.3 m sec^{-1}).

STATISTICAL ANALYSIS

We used analyses for circular distributions to generate descriptive statistics and test hypotheses concerning nest orientation. We calculated the mean angle ($\bar{a}$), or bearing, and angular deviation (s) (Zar 1999) of nest orientation for each species and of wind direction. We used Rayleigh's test of uniform distribution for nest orientations within each species and wind direction and the Watson–Williams two-sample test for differences between the species in nest orientation. We obtained approximate P values for each hypothesis test by using 5000 random permutations for each test, calculating them with macros created by M. Kölliker (Kölliker and Richner 2004; http://evolution.unibas.ch/koelliker/misc.htm) for use in the SAS system (SAS Institute 2003). To test the prediction that seasonal shifts in nest orientation coincide with seasonal shifts in prevailing wind direction, we used an angular–linear correlation (Zar 1999) to compare nest orientation to the Julian date of nest initiation and to compare wind direction to Julian date. Correlations of nest and wind orientations with date were determined with data pooled across years and separately by year, the latter to explore the possibility of annual variation in wind direction and how such variation might be associated with seasonal shifts in nest orientation. A statistical significance threshold was set at $\alpha = 0.05$ for each hypothesis test.

RESULTS

We determined the orientation of 333 Grasshopper Sparrow and 272 Eastern Meadowlark nests. The mean orientations of Grasshopper Sparrow ($\bar{a} = 33.4°$, $s = 66.4$, $P < 0.001$) and Eastern Meadowlark ($\bar{a} = 52.9°$, $s = 69.5$, $P < 0.001$) nests were significantly nonrandom, being primarily to the northeast (Fig. 1). The mean orientation of Grasshopper Sparrow and Eastern Meadowlark nests differed from each other only marginally ($F_{1, 603} = 2.5$, $P = 0.1$). In 2004 the orientation of Grasshopper Sparrow nests shifted significantly eastward over the nesting season (Table 1). In 2005, it shifted northward, but this shift was only marginally significant. In the Eastern Meadowlark, nest orientation and nest-initiation date were significantly and positively correlated in 2004 and when data from both years were pooled (Table 1). In both cases, meadowlark nests were pointed more to the east before the median date of nest initiation and shifted northward later in the season (see Table 1 for median nest-initiation dates). Despite significant correlations between nest orientation and date in both species, correlation coefficients (r) were generally low (≤0.24; Table 1), indicating much unexplained variation in nest orientation.

Mean prevailing winds were generally from the south (both years pooled, $\bar{a} = 171.1°$, $s = 51.6$, $P < 0.001$) (Fig. 1). In both years of study wind direction shifted significantly from the south-southwest to south-southeast as the nesting season progressed (Table 1).

DISCUSSION

Entrances of Grasshopper Sparrow and Eastern Meadowlark nests were oriented toward the northeast, generally away from the prevailing southerly winds. In addition to any thermoregulatory advantages, orienting nest entrances with the direction of wind-blown grasses might provide birds with some structural advantage in constructing nest domes (Lanyon 1957, Roseberry and Klimstra 1970) or aid adults in leaving or entering nests. Mean nest orientation was not directly downwind, however. Additionally, seasonal shifts in nest orientation did not track seasonal shifts in wind direction similarly in the two species. Orientation of meadowlark nests shifted northward as wind direction shifted southeastward. Conversely, orientation of Grasshopper Sparrow nests shifted slightly eastward in one year of study. Therefore, wind is likely not the only factor influencing nest orientation.

Shading from the afternoon sun may also be important, and it is possible that birds orient nests opposite the solar angle, contributing to deviations from the tendency to orient nests downwind. Burton (2007) suggested that the predominance of east-facing nest orientations in ground-nesting birds of middle latitudes reflects an avoidance of detrimental solar radiation (Lloyd and Martin 2004) from the west during warm afternoons and promotes warming during cooler mornings. For nests of *Anas* ducks and the Short-eared Owl (*Asio flammeus*) in grasslands, Hoekman et al. (2002) found a seasonal shift in nest orientation relative to vegetative cover and suggested that these birds were using afternoon shade in response to seasonal

TABLE 1. Results from angular–linear correlations of orientation of Grasshopper Sparrow and Eastern Meadowlark nest entrances and wind direction with date of the nesting season.[a]

	Period	n[b]	r	χ^{2}[c]	P	$\bar{a}$ before nest initiation[d]	$\bar{a}$ after nest initiation[d]
Grasshopper Sparrow	Years pooled	333	0.080	2.157	0.3	36.7° ± 67.0°	30.2° ± 65.8°
	2004	169	0.234	9.229	<0.1	28.3° ± 70.5°	47.8° ± 65.2°
	2005	164	0.186	5.681	0.1	42.1° ± 63.0°	12.9° ± 64.7°
Eastern Meadowlark	Years pooled	272	0.242	16.001	<0.001	66.7° ± 71.9°	44.1° ± 66.5°
	2004	127	0.218	6.051	<0.1	66.6° ± 69.6°	36.6° ± 61.3°
	2005	145	0.165	3.945	0.1	66.9° ± 74.1°	54.4° ± 70.1°
Wind direction	Years pooled	184	0.200	7.391	<0.1	193.1° ± 57.2°	157.8° ± 59.8°
	2004	92	0.263	6.350	<0.1	189.8° ± 54.3°	145.5° ± 74.2°
	2005	92	0.410	15.492	<0.001	196.9° ± 59.9°	160.5° ± 39.8°

[a]Median nest initiation dates were 27 and 24 May for Grasshopper Sparrow in 2004 and 2005, respectively, and 19 and 17 May for Eastern Meadowlark in 2004 and 2005, respectively. The season's (1 May–31 July) midpoint (median date) for wind-direction data in each year was 15 June.
[b]Nests for birds, days for wind.
[c]df = 2 for all correlations.
[d]Mean orientation angle and angular deviation ($\bar{a} \pm s$).

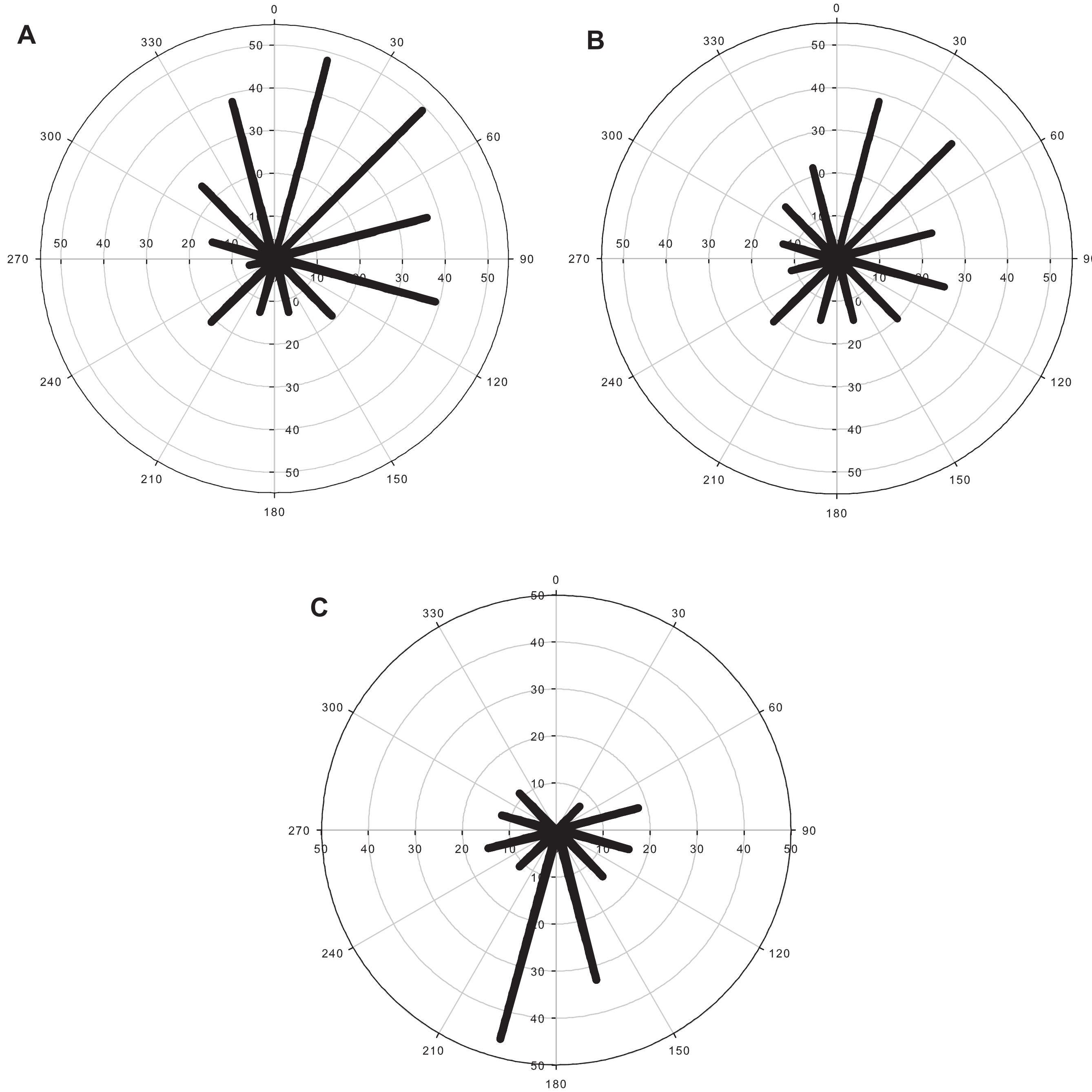

FIGURE 1. Orientations of Grasshopper Sparrow (A) and Eastern Meadowlark (B) nest entrances, and orientation of wind direction (C). Bars along radial axes indicate numbers of nests (A, B) or numbers of days of wind direction measurements (C) within 30° intervals along peripheral axes (see text).

changes in solar angle. Perhaps the northward shift in nest orientation that we observed for Eastern Meadowlarks later in the season reflects the increasing importance of shade during the later, warmer portion of the nesting season and a prevailing southern solar angle.

The basis for the discrepancy between species in the seasonal shift in nest orientation is unclear. Structurally, the nest entrance is arguably the least aerodynamic side of the nest domes of these species. In addition to possibly responding to the changing solar angle (above), perhaps the taller Eastern Meadowlark nest is more prone to being damaged by strong winds, necessitating a northward shift of nest-entrance orientation to track the shift in the prevailing wind direction. The Grasshopper Sparrow's smaller nest, like that of some other ground-nesting species (With and Webb 1993), may be sheltered from wind merely by virtue of its low stature.

Our study demonstrates nonrandom patterns of nest-dome orientation in the Grasshopper Sparrow and Eastern Meadowlark.

There appears to be some relation to wind direction, though we observed much variation in nest orientation (Fig. 1). There are likely many other environmental factors that lack a strong directional component but nonetheless contribute to variation in nest orientation. For example, the dome-shaped nests of the Eastern Meadowlark (Roseberry and Klimstra 1970) and Ovenbird (*Seiurus aurocapilla*) (Van Horn and Donovan 1994) tend to face downhill, perhaps aiding in efficient exits from nests. Some of our study sites were hilly, which may have influenced the orientation of Grasshopper Sparrow and Eastern Meadowlark nests. Some species may orient their nests toward males' song perches. Promiscuous female Black-capped Chickadees (*Poecile atricapillus*) tend to excavate nest cavities in the direction of extrapair males (Mennill and Ratcliffe 2004). Eastern Meadowlark nests, however, appear not to be oriented toward song perches (Lanyon 1957); we are unaware of such evidence for the Grasshopper Sparrow. Nest orientation appears to be sensitive to environmental factors and deserves further exploration.

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