MICROCLIMATE OF GROUND NESTS: THE RELATIVE IMPORTANCE OF RADIATIVE COVER AND WIND BREAKS FOR THREE GRASSLAND SPECIES[1]

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Abstract. Three species of ground-nesting birds of the shortgrass prairie demonstrate contrasting strategies in nest placement: nests of Lark Buntings (*Calamospiza melanocorys*) are situated beneath shrubs or bunch grasses, whereas nests of McCown's Longspurs (*Calcarius mccownii*) and Horned Larks (*Eremophila alpestris*) are associated with sparse cover and are relatively exposed. Nests of these species exhibited a reduction in ambient wind velocity by at least an order of magnitude. Spatial orientation of vegetation around nests did not indicate the degree to which nests were sheltered from wind, however. Nests of Lark Buntings were placed on the leeward side of shrubs, but vegetation apparently did not function as wind breaks. Profiles of the relative wind velocity at nests (nest-cup versus ambient wind velocities) documented that exposed nests of longspurs and Horned Larks were more sheltered from wind than nests of Lark Buntings.

The association of bunting nests with overhanging vegetation instead may be in response to radiative cover. Nests of Lark Buntings were completely shaded 60% of the day compared to 45% for nests of longspurs and larks. Furthermore, bunting nests were shaded 40% of midday hours when solar intensity was at a maximum; nests of longspurs and larks were shaded only 5% and 13%, respectively, during this period.

Buntings begin breeding later in the season than either longspurs or Horned Larks and thus are exposed to higher ambient temperatures and decreased winds. Buntings are unique among the three species in that males incubate. Given that males have black plumage, opportunities for radiative cover and convective cooling may be important for nest placement in this species. In contrast, early-nesting longspurs and larks may accrue thermal benefits from increased exposure of nests to solar radiation.

Key words: Grassland birds; ground nests; microclimate; nest-site selection; radiative cover; wind breaks.

INTRODUCTION

Amelioration of climatic factors is a major determinant of nest-site selection in birds (e.g., Walsberg 1985). Nevertheless, the microclimate of nests is one of the least-studied aspects of site selection. Evaluation of the thermal environment at nests has taken one of two forms. The thermal dynamics at nest locations and the consequences for nest occupants have been assessed via biophysical modelling (e.g., Calder 1973, Walsberg and King 1978, Webb and King 1983), but this approach has been applied to only a handful of species (Walsberg 1985). More generally, avian ecologists have characterized nest sites according to floristic and physiognomic features of the microhabitat, and have then speculated about potential thermal (as well as other) advantages that presumably dictate nest placement (e.g., Giesen et al. 1980, Rich 1980, Cannings and Threlfall 1981, Reynolds and Knapton 1984, Page et al. 1985, Petersen and Best 1985, Beckoff et al. 1987, Sakai and Noon 1991).

Novel insights into factors responsible for nest-site selection may be gained by merging these two approaches and quantifying the thermal environment of nest microhabitats for different species in the same habitat. To bridge this gap, we assessed the relative importance of microclimatic factors in relation to vegetative cover at nest sites for three species of ground-nesting birds in a semi-arid grassland: the McCown's Longspur (*Calcarius mccownii*), Horned Lark (*Eremophila alpestris*), and Lark Bunting (*Calamospiza melanocorys*). Nests of Lark Buntings are

always situated beneath cover afforded by bunch grasses or shrubs, whereas nests of McCown's Longspurs and Horned Larks are relatively exposed, although they are typically associated with at least peripheral vegetation or other structural features of the prairie (e.g., cow pats; Creighton and Baldwin 1974, pers. observ.). Given that the shortgrass prairie is characterized by wind and subjected to intense solar radiation during the breeding season, our assessment of nest microclimate focused on these two climatic phenomena. Convection and short-ware radiation further were shown to be the two most important routes of heat transfer for eggs and nestlings of open-nesting species (Webb and King 1983). We therefore reasoned that if nest placement functioned to ameliorate adverse microclimatic effects, site selection in this habitat would most likely be based on the potential for wind breaks and radiative cover.

METHODS

STUDY AREA

The Central Plains Experimental Range (CPER) is a Long-Term Ecological Research site that encompasses 6,280 ha of shortgrass prairie in northcentral Colorado. The CPER is located 50 km northeast of Fort Collins in Weld County at an elevation of 1,650 m. The site is subdivided into 130-ha pastures that have been subjected to different intensities of cattle grazing since 1939. Average annual precipitation is 311 ± 85 (SD) mm ($n = 45$ years), with 85% of the precipitation occurring from May through July (Milchunas and Lauenroth 1989). Monthly temperatures range from a mean maximum of 31°C in July to a mean minimum of −12°C in January.

Temperature profiles throughout the 1991 breeding season (approximately late April–late July; Julian dates = 120–210) indicated that minimum temperatures did not consistently remain above 0°C until mid-May (Julian date = 135). Temperatures exceeding 30°C were encountered initially in mid-June (Julian date = 169), but average daily temperatures did not remain over 20°C until a week later (Julian date = 176). Strong winds (e.g., 10 m/sec at 1 m) were a feature of the early weeks of the breeding season (Julian date $\leq$ 140). Winds are primarily from the northwest and southeast at the CPER. Winds from either direction coincided with the movement of major weather fronts into the area.

To ensure that our study area represented a range of habitat in which the three bird species nested, a 10-ha plot was established in each of two pastures: a moderately grazed (MG) pasture (26NW), in which 40% of annual growth is consumed by cattle, and a heavily grazed (HG) pasture (23E), in which 60% of annual growth is consumed. In general, the shortgrass prairie is dominated by perennial grasses (primarily *Bouteloua gracilis* and *Buchloe dactyloides*), which are interspersed with midgrasses (e.g., *Aristida longiseta* and *Stipa comata*), forbs (e.g., *Eriogonum effusum*), shrubs (e.g., *Chrysothamnus nauseosus* and *Gutierrezia sarothrae*), and cactus (e.g., *Opuntia polyacantha*) (Jameson 1969). Grazing had the effect of producing a uniform, lawn-like physiognomy in the HG pasture (Milchunas and Lauenroth 1989). Lark Buntings did not breed on this plot, whereas all three species nested on the MG plot.

NATURAL HISTORY OF SPECIES

All three species build a cup-shaped nest of grass built within a shallow depression in the ground. Nest diameter is related to body size, but the smallest species, the McCown's Longspur, possesses the deepest nest (Table 1; Harrison 1979). Clutch sizes of longspurs and Horned Larks are similar, consisting of two to four eggs per clutch (McCown's Longspur, 1991: $\bar{x} = 3.0 \pm 0.66$ (SD), $n = 52$ nests; Horned Lark: $\bar{x} = 2.8$, $n = 34$, Strong and Ryder 1971). Lark Buntings have larger clutches on average and lay from two to six eggs per clutch ($\bar{x}$: 4.0, $n = 30$; Strong and Ryder 1971). The blue eggs of Lark Buntings are distinctly different in color from those of the other two species, whose eggs have brown spots or scrawls on a gray background. Peak nesting dates differ among the three species owing to different arrival times on the study area (Table 1). Horned Larks are present throughout the year, but it is not certain whether the population that is breeding at the CPER is the same that winters there (Strong and Ryder 1971). The Lark Bunting is unique among the three species in that both sexes incubate, albeit disproportionately; females were reported on the nest 70% of the time (Creighton 1971).

Nest-site microhabitat differed among the three species. In the MG pasture, a third of the longspur nests (32%, total $n = 31$) were placed beside *Aristida*, 19% were associated with *Opuntia*, and 13% were associated with *Gutierrezia* and *Stipa*

each. In the HG pasture, nests were primarily (59%, $n = 22$) associated with *Opuntia*; 18% of the nests were associated with *Gutierrezia*. Although based on a small sample ($n = 10$, both pastures combined), nests of Horned Larks were found to be most often associated with cow pats (40%) in this study. Nests of Lark Buntings are always closely associated with vegetation that overhangs the nest (*Aristida* was associated with 63% of nests [$n = 43$] in Creighton [1971] and with 49% of nests [$n = 90$] in Creighton and Baldwin [1974]; the latter study also documented nests associated with *Chrysothamnus* [26%]).

DATA COLLECTION

Nest orientation. We measured the orientation of nests (relative to magnetic north) for comparison with the direction of the prevailing winds during the incubation period; all nests of the three species located during censuses in 1990 and 1991 on the two pastures were used in this context. The "entrance" of the nest was defined as the area around the nest not covered with vegetation and which was used by the adults when entering or exiting the nest. Nest orientation was recorded as the direction bisecting the entrance of each nest.

Nest microclimate. Five nests each for Mc-Cown's Longspurs and Lark Buntings, and seven nests of Horned Larks, were selected arbitrarily for a comparison of nest microclimate among the three species. Because collecting data on the microclimate of nest sites could interfere with reproductive success, we collected data after the nests were no longer active. The physical structure of vegetation associated with nests was still intact, although the vegetation might have become senescent in the interim.

Shelter from wind. We compared the spatial orientation of vegetation around the nest with the mean daily direction of wind throughout the incubation period of each nest to assess whether vegetation appeared to function as wind breaks. Wind direction was recorded from a height of 1 m above the ground at the meteorological station at the CPER; the mean daily wind direction was obtained by averaging wind direction (using circular statistics; Zar 1984) over data collected at 1-hr intervals throughout the day. In addition, we obtained wind profiles for each nest by simultaneously measuring wind velocities inside the nest cup and 1 m above the nest on 23–24 June 1991 for longspurs and larks, and on 2 Au-

TABLE 1. Reproductive characteristics for three ground-nesting bird species of the shortgrass prairie.

Species	Body mass[a] (g)	Peak date of nesting[b]	Modal clutch size	Length of incubation[c] (days)	Type of incubation[d]	Nest dimensions[e] Diameter (cm)	Nest dimensions[e] Depth (cm)	Nest microhabitat
McCown's Longspur	25	bimodal: mid May and mid June	3	12	female only	6.4	5.4	exposed nest; beside midgrasses, cactus
Horned Lark	34	late April to early May	3	12	female only	5.1 × 6.4	3.8	exposed nest; beside sparse vegetation or cow pats, shortgrasses, cactus
Lark Bunting	36	bimodal: late May and mid June	4	12	biparental	6.9	3.8	extensive nest cover; beneath midgrasses, shrubs

[a] Giezentanner 1970.
[b] McCown's Longspur: Porter and Ryder 1974, pers. observ.; Horned Lark and Lark Bunting: Creighton and Baldwin 1974.
[c] Creighton 1971, Creighton and Baldwin 1974.
[d] McCown's Longspur: Creighton and Baldwin 1974, pers. observ.; Horned Lark: Bent 1942; Lark Bunting: Creighton 1971, pers. observ.
[e] Harrison 1979.

gust 1991 for buntings. Wind speed within the nest cup was measured using a Kurz heated ceramic-element anemometer (sensitivity = 0.01 m/sec) (model 1440; Kurz Instruments, Inc., Monterey, California). Wind speed outside the nest was measured with a Thornthwaite cup anemometer (stall speed < 0.15 m/sec) (C. W. Thornthwaite Associates, Lemur, New Jersey). The Kurz and Thornthwaite anemometers are omnidirectional in a horizontal plane. Manufacturers' calibration curves were used for both types of anemometers; anemometers were previously calibrated against a Pitot tube in a wind tunnel to check manufacturers' calibration curves. Measurements of wind velocity were recorded at 1-sec intervals and averaged over 1 min for a period of approximately 30 min at each nest with a Campbell Scientific CR-10 digitizing datalogger (Campbell Scientific, Inc., Logan, Utah).

Radiative cover. Degree of shading from solar radiation provided by vegetation at each nest was measured by using a "fisheye" photograph taken from the center of the nest; the photograph provided a complete angle coverage of 180° (Walsberg 1981). Photographs were taken between 6 September and 18 September 1991 with a custom-manufactured device composed of a Li-Cor Optical Sensor Head (LAI-2050, Li-Cor, Inc., Lincoln, Nebraska) that was mounted on a custom-manufactured adaptor for a Nikon camera body. We overlaid enlarged photocopies of the photographs with the hourly sun track for the dates of the incubation period for each nest and the proper latitude (List 1951). To quantify the radiative view of the nest during the incubation period, we measured the proportion of each hour throughout the day that the nest was completely shaded along the sun track for each nest with a digitizing program.

Egg reflectance. Because the thermal physiology of eggs strongly affects parental attentiveness at the nest (Webb and King 1983, Zerba and Morton 1983), we attempted to provide a more comprehensive understanding of the abiotic conditions affecting nesting adults by obtaining egg-reflectance values for each species. The reflectance of three eggs from each of five clutches for each species (clutches obtained from the Denver

Museum of Natural History; clutches used were collected in or near Weld Co.) was measured using a Li-Cor pyranometer sensor (LI-200SZ) fitted with a long tube (diameter = 0.9 cm, length = 5.1 cm) that restricted the field of view to 10°. Egg-shaped spheres were covered with paints of known reflectance values and used as standards in order to obtain percent reflectivity of eggs. Percent reflectivity was obtained by regressing the measured reflectance values and the percent reflectivity of the known standards (e.g., reflectance value for black = 220, 1.5% reflectivity; brown = 254, 14.1%; white = 314, 68%). The regression equation for this relationship was: y = 225.8 + 1.324 (Percent Reflectance). Our measurements assessed reflectance in the short-wave spectrum, and may not include effects in the infrared (Bakken et al. 1978).

DATA ANALYSIS

Nest orientation. As no significant differences in orientation of nests were found between years or pastures ($P > 0.05$, Watson-Williams Test; Zar 1984:446–448), data from different years and pastures were pooled for each species in subsequent analyses. To test for differences in nest orientation among the three species, we performed an extension of the Watson-Williams Test for three samples. We assessed whether nest orientations comprised a random distribution for each species via Rayleigh's Test (Zar 1984:442–443). Where the hypothesis of a random distribution was rejected, we tested the hypothesis of a northern orientation (0°) for each species using a one-sample test with 95% confidence limits (Zar 1984:445–446).

NEST MICROCLIMATE

Shelter from wind. Several problems constrained our analyses of the degree to which nests were sheltered from wind: (1) Repeated measurements were made on each nest and data are serially correlated; (2) Because each nest was not measured over the same range of wind conditions, an individual nest may contribute disproportionately to the shape of the relationship (Fig 1); and (3) Residuals of the wind relationship at nest sites for each species indicate departures from

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FIGURE 1.   Relative wind velocities at nest sites for three species of grassland birds: McCown's Longspur (n = 5 nests), Horned Lark (n = 7), and Lark Bunting (n = 5). Wind velocity was measured inside the nest cup and 1 m above the nest. Residuals were generated by linear regression. Symbols represent individual nests.
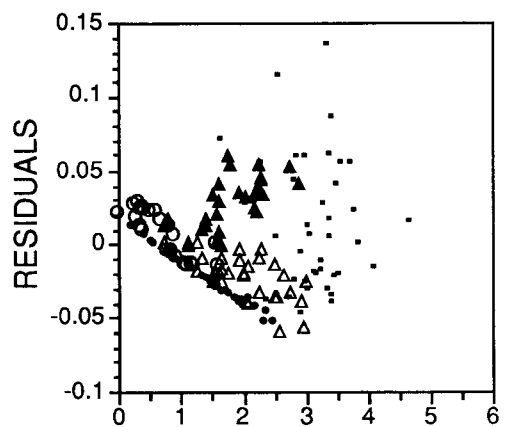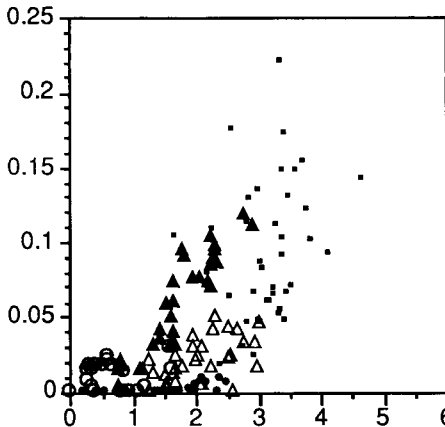
MCCOWN'S LONGSPUR
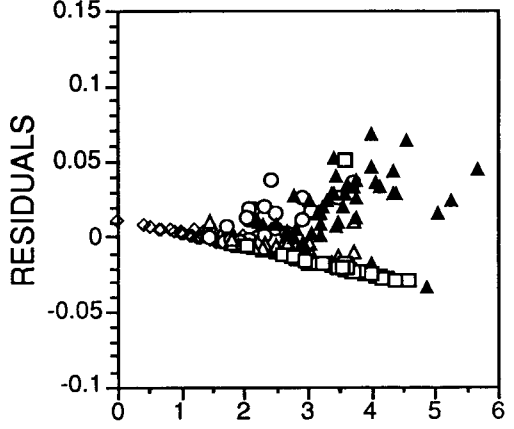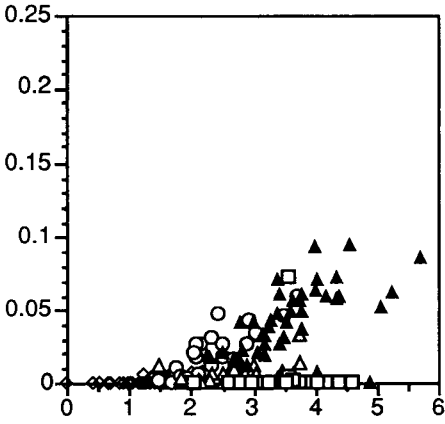
HORNED LARK
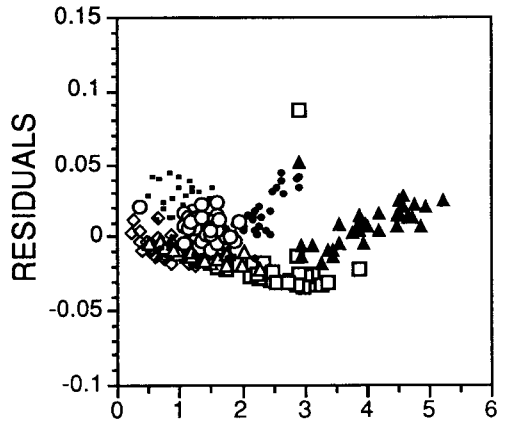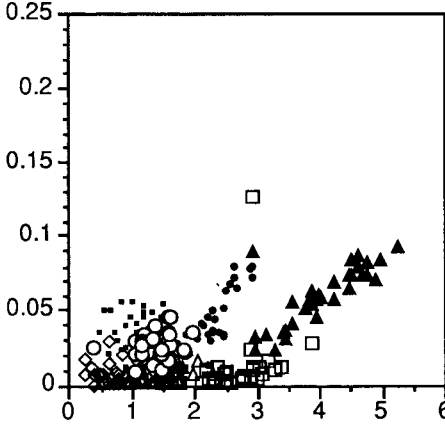
LARK BUNTING

WIND VELOCITY INSIDE NEST CUP (m/s)

RESIDUALS

WIND VELOCITY OUTSIDE NEST CUP (m/s)

normality and homoscedascity (Fig. 1). The graphs of residuals further indicate the existence of a threshold. Below some threshold level, wind is absent within nest cups despite ambient winds. Beyond this threshold, however, wind velocity inside the nest cup increases as a non-linear function of the ambient wind velocity.

To circumvent these problems, we obtained a ratio of wind speeds (ratio of wind velocities inside nest cup versus outside nest) for each nest; this dimensionless unit preserves the proportional contribution of the ambient wind to the wind speed inside the nest (L. Hipps, pers. comm.). We then subjected the distribution of ratios for each species to log-linear analysis (Fienberg 1980) to assess the contribution of individual nests; by factoring out the variance attributable to individual nests in the development of the log-linear model, we addressed the concern of repeated measures on nests and the potential for disproportionate contributions of individual nests to the overall relationship. We then were able to address our primary question of the degree to which nests of different species are sheltered from the wind. Because log-linear analysis does not support unbalanced sampling designs (SAS Institute, Inc. 1988:238), two Horned Lark nests, selected at random, were omitted from analysis.

Radiative cover. Differences among species in the degree of radiative cover of nests were assessed via time-series analysis, using a three-step moving average (Wonnacott and Wonnacott 1984:219) of the average proportion of time nests of the three species were shaded throughout the day during the incubation period. This results in a "smoothing" of the nest-shading curves by averaging over the variance for which we could not control, such as the spatial variation attributable to individual nest locations and errors in our estimates of shading recorded from the sun tracks for each nest. The response curves resulting from this time-series analysis enabled us to compare the shade profiles for nests among the three species.

Egg reflectance. We tested the difference in egg reflectance among species via a nested Analysis of Variance (ANOVA) on log-transformed data; the variation attributable to individual clutches was nested within the effects of species. Multiple comparisons between species were performed using Tukey's Studentized Range.

RESULTS

NEST ORIENTATION

Species exhibited nonrandom orientation in nest placement (McCown's Longspur: $z = 45.78$, $n = 78$, $P < 0.001$; Horned Lark: $z = 5.38$, $n = 10$, $P < 0.01$; Lark Bunting: $z = 4.204$, $n = 16$, $P < 0.05$; Rayleigh's Test). Nests of McCown's Longspurs and Lark Buntings had a significant northern orientation (McCown's Longspur: $\bar{x} = 5.8°$ $\pm 6°$; Lark Bunting: $\bar{x} = 12.7° \pm 41°$; one-sample test with 95% confidence intervals), whereas nests of Horned Larks exhibited a significant northeast (45°) orientation ($\bar{x} = 44.4 \pm 32°$). Species did not differ in the orientation of nest placement, however ($F = 3.01$, df $= 2,101$, $P > 0.05$; Watson-Williams Test).

NEST MICROCLIMATE

Shelter from wind. Given that prevailing winds in this system are generally from the northwest or southeast and our analyses on nest orientation indicated that the "entrances" of nests faced north, the spatial distribution of vegetation should circumscribe some area of the nest from approximately 45° to 315° if nest placement provides wind breaks. The spatial orientation of vegetation around nests did not always coincide with the prevailing wind direction, however (Figs. 2–4). Nests of McCown's Longspurs were sheltered on the southeast side in three of five nests, whereas two nests (Nest #17, 26NW and Nest #5, 23E) appeared completely exposed to prevailing winds (Fig. 2). Vegetation afforded little (Nest #1, 26NW) or no (Nest #1, 23E) protection from wind in some Horned Lark nests (Fig. 3). Because nests of Lark Buntings are associated with substantial vegetative cover (e.g., shrubs), a greater proportion of nest area was edged with vegetation than in the other two species (Fig. 4).

The spatial orientation of vegetation around nests, however, may have little effect on the degree to which nests are sheltered from wind. Wind profiles for nests of the three species clearly show that the relatively exposed nests of McCown's Longspurs are the most protected from ambient winds (high frequency of small relative wind-ratio values; Fig. 5), whereas the seemingly well-sheltered nests of Lark Buntings are the least protected (Figs. 1 and 5). Nests for all species exhibited a reduction of wind velocity that was at least an order of magnitude less than ambient

26 NW--Nest #20

26 NW--Nest #17

23 E--Nest #5
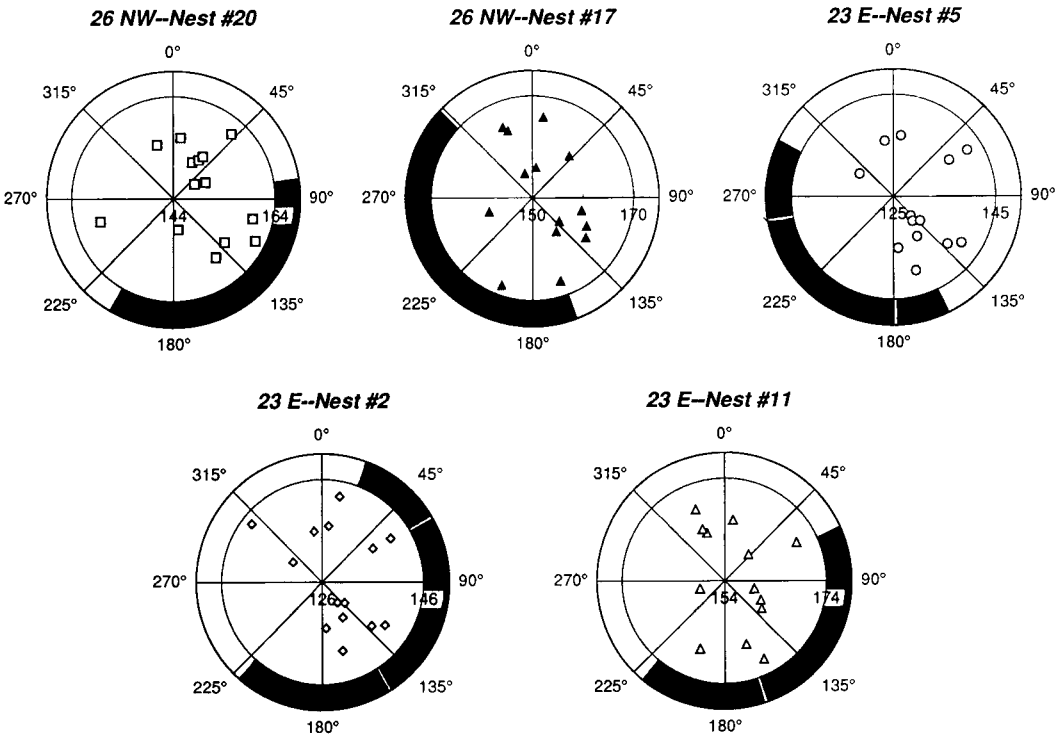
23 E--Nest #2

23 E--Nest #11

FIGURE 2.   Spatial orientation of vegetation (outer shaded region of diagrams) of individual nests for McCown's Longspurs, relative to the average daily wind direction (symbols) at the Central Plains Experimental Range throughout the incubation period (Julian date on axis) of each nest. The scatter of points thus represents the directionality of wind throughout the incubation period of each nest. Distance of symbols from the center of each diagram represents the Julian date of the incubation period (e.g., mean wind direction for Julian date 145 is closer to center than that for 162). Symbols are specific for individual nests, and are the same as those used for McCown's Longspurs in Figure 1.

winds, however (Fig. 1). Log-linear analysis documented that wind profiles differed significantly among the three species (Species × Wind Ratio: $G = 78.67$, df = 10, $P < 0.001$), although the fact that the three-way interaction term (Species × Nest × Wind Ratio) was significant ($G = 127.61$, df = 40, $P = 0.000$) indicates that there is also marked variation among individual nests within species.

Radiative cover. Nests of McCown's Longspurs and Horned Larks were almost completely exposed to solar radiation during the middle of the day (McCown's Longspur: 09:00–14:00, $\bar{x}$ proportion of time shaded during this period = 0.05 ± 0.047; Horned Lark: 10:00–15:00, $\bar{x}$ = 0.13 ± 0.063; Fig. 6A). In contrast, nests of Lark Buntings were never exposed to the sun for longer than 48 min during a 1-hr period (proportion

of time shaded always >0.20; $\bar{x}$ proportion of time shaded from 09:00–15:00 = 0.41 ± 0.160; Fig. 6A). Smoothing of the shade profiles for nests of the three species via time-series analysis presents a clearer picture of nest insolation (Fig. 6B). Until 07:00 (time step 2), nests of all species were well shaded, resulting in a congruence among response curves. Between 07:00 and 10:00 (time steps 3–5), however, longspur nests exhibited a marked increase in solar exposure compared to the other two species. During time step 6 (09:00–11:00), nests of Horned Larks were more exposed than those of buntings. By time step 8 (11:00–13:00), the shade profile of lark nests converged with that for longspur nests. Actually, the shade profiles for longspurs and larks were very similar, as the response curve for lark nests suggests a "phase shift" of 1 hr relative to longspur nests.
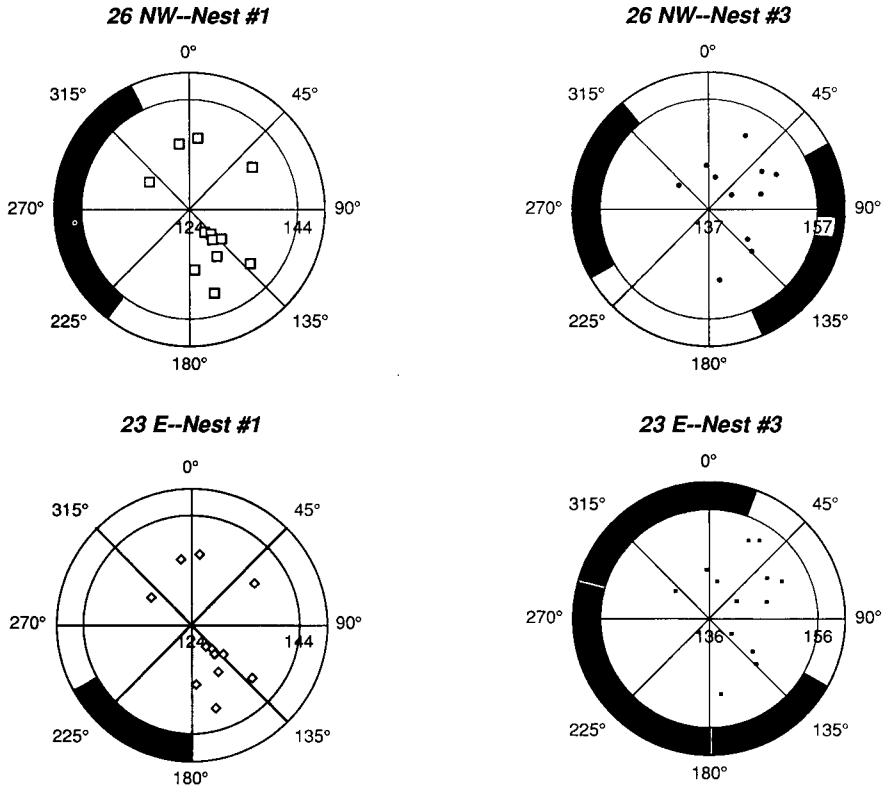
FIGURE 3.   Spatial orientation of vegetation (outer shaded region of diagrams) of individual nests for Horned Larks, relative to the average daily wind direction (symbols) at the Central Plains Experimental Range throughout the incubation period (Julian date on axis) of each nest. See caption for Figure 2 for further clarification. Symbols are specific for individual nests, and are the same as those used for Horned Larks in Figure 1.

EGG REFLECTANCE

Eggs of Horned Larks reflected nearly 60% of solar radiation ($\bar{x} = 59.3 \pm 3.83\%$), whereas eggs of McCown's Longspurs were the least reflective of the three species with 53% reflectivity ($\bar{x} = 52.7 \pm 3.47\%$); Lark Buntings were intermediate with eggs of 56% reflectivity ($\bar{x} = 56.3 \pm 2.76\%$). Egg reflectance differed significantly among the three species ($F = 40.1$, df $= 2,30$, $P < 0.001$; nested ANOVA), although individual clutches within a species also exhibited significant variability in egg-reflectance values ($F = 13.39$, df $= 12,30$, $P < 0.001$).

DISCUSSION

THE IMPORTANCE OF WIND BREAKS

Evidence for the importance of wind breaks at nests of these three grassland bird species was equivocal. Nests of all three species exhibited at least an order-of-magnitude reduction of ambient wind velocity, but the spatial orientation of vegetation circumscribing nests did not always coincide with prevailing wind directions. Wind profiles of the relatively exposed nests of McCown's Longspurs and Horned Larks clearly document a reduction in nest-cup wind velocities relative to ambient winds. Paradoxically, nests of Lark Buntings, which seemed to be well sheltered by vegetation, exhibited less amelioration of wind compared to nests of the other two species (Figs. 1, 5). Ground nests in general are expected to experience some reduction in wind by virtue of the fact that they are placed within the boundary layer of the ground; in the same study area, Graul (1975) documented a 3.5-fold increase in average wind velocity at 7 cm above ground relative to ground level. Microhabitat data on the relative position of nests with respect to vegetation thus provided an incomplete and per-

Nest #1

Nest #4
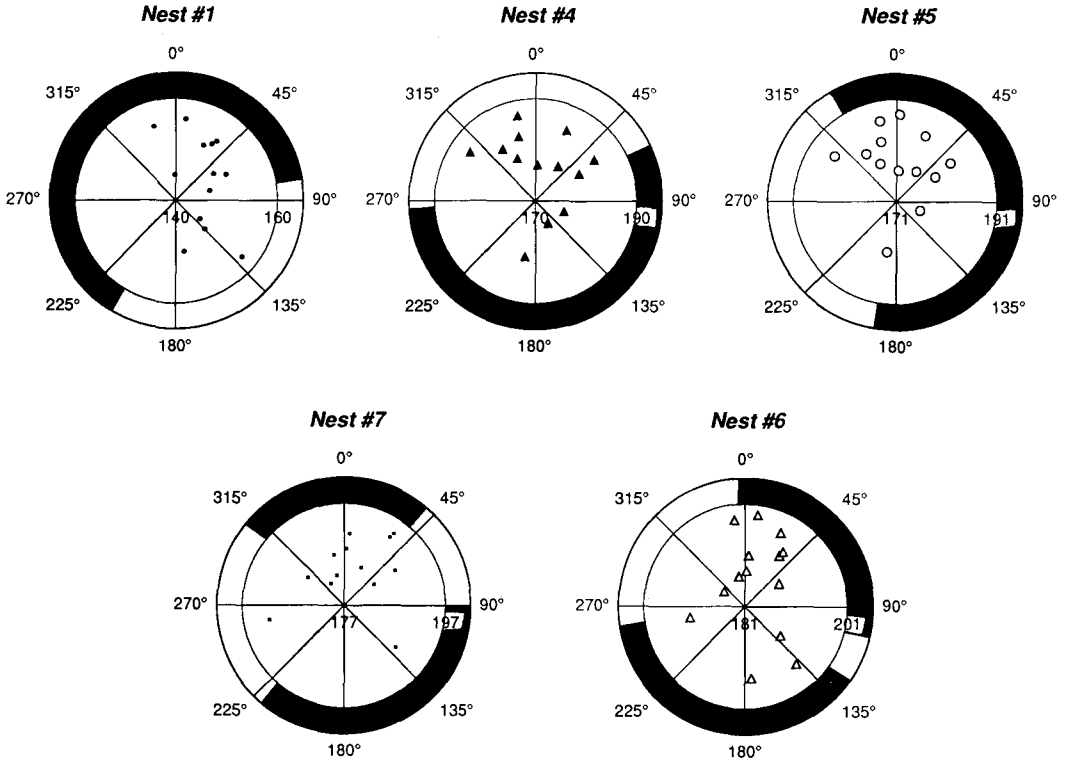
Nest #5

Nest #7

Nest #6

FIGURE 4.   Spatial orientation of vegetation (outer shaded region of diagrams) of individual nests for Lark Buntings, relative to the average daily wind direction (symbols) at the Central Plains Experimental Range throughout the incubation period (Julian date on axis) of each nest. See caption for Figure 2 for further clarification. Symbols are specific for individual nests, and are the same as those used for Lark Buntings in Figure 1.

haps misleading picture of the degree to which nests were sheltered from wind.

An experiment we performed to alter the airflow dynamics over a Horned Lark nest suggests that associated structures play a minor role as wind breaks for ground nests. This nest was beneath the lip of a cow pat, and removal of the cow pat did not significantly alter the wind profile for this nest ($\chi^2 = 1.3$, df $= 4$, $P > 0.05$; Chi-square Analysis). Although cow pats do not present a vertical barrier to wind as might a cactus pad or clump of grass, some disruption of air flow over the nest should occur. Because log-linear analysis suggested that significant variation in wind profiles occurred among nests within a species, we cannot entirely dismiss the possibility that vegetation affords some shelter from wind. The variability in wind profiles for individual nests might be attributable to the different range of conditions over which they were mea-

sured, however, rather than to differences in spatial orientation or type of associated vegetation.

THE IMPORTANCE OF RADIATIVE COVER

The degree of radiative cover appears to be a more important consequence of nest placement in this system. Nests of buntings were completely shaded nearly 60% of daylight hours ($\bar{x} = 58.4 \pm 29.2\%$), whereas nests of longspurs and Horned Larks were shaded only 45% of the day ($\bar{x} = 43.9 \pm 36.8\%$ and $\bar{x} = 44.6 \pm 31.6\%$, respectively). In fact, nests of longspurs and larks were almost completely exposed during the middle of the day when solar intensity was at its maximum. Amelioration of heat stress by maximizing radiative cover of the nest has been documented in White-crowned Sparrows (*Zonotrichia leucophrys*), where the vegetative canopy over the nest occluded 62% of the sky and nests experienced 1.7
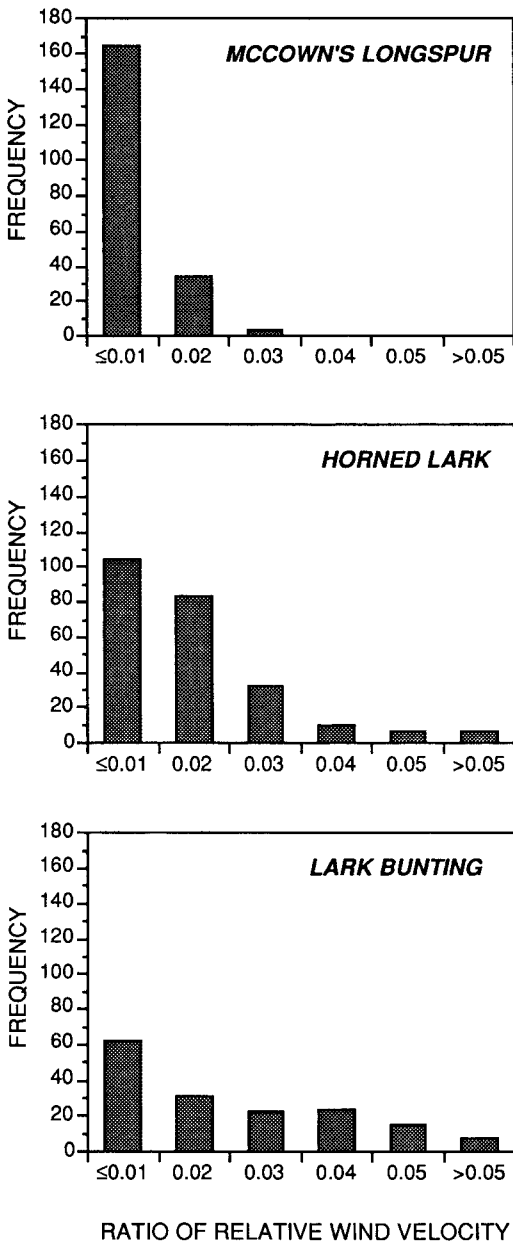
RATIO OF RELATIVE WIND VELOCITY

FIGURE 5. Wind profiles for nests of three species of grassland birds: McCown's Longspur (n = 5 nests), Horned Lark (n = 5), and Lark Bunting (n = 5). The wind-velocity ratio is the wind velocity inside the nest cup divided by the ambient wind velocity 1 m above the nest.

times more solar radiation before noon than after noon (Walsberg and King 1978). Radiative cover was also important in minimizing heat stress in eggs and nestlings of this same species (Webb

and King 1983). In Warbling Vireos (*Vireo gilvus*), nests were positioned in woodland canopies such that solar radiation was reduced by 47% during the afternoon hours (Walsberg 1981). These examples parallel the nest placement of Lark Buntings in the shortgrass prairie, which likewise exhibited a 40% reduction in exposure to solar radiation during the afternoon.

The contrasting patterns of nest placement with respect to radiative cover between buntings and longspurs/larks are not attributable to differences in nest orientation. All species exhibited a northern orientation (interestingly, a population of Horned Larks in Newfoundland exhibited a northeast nest orientation, as did the lark population of our study; Cannings and Threlfall 1981). Directional biases in nest orientation generally have been interpreted as conferring some thermal advantage, and the literature is replete with examples, particularly for cavity-nesting species (e.g., Connor 1975, Crockett and Hadow 1975, Inouye 1976, Inouye et al. 1981, but see Korol and Hutto 1984, Kerpez and Smith 1990) or species that build enclosed nests (Ricklefs and Hainsworth 1969; Austin 1974, 1976; McGillivray 1981). Orientation of open nests with respect to some vegetative structure presumably represents the exploitation of some thermal advantage (e.g., Balda and Bateman 1973, Reynolds and Knapton 1984, Petersen and Best 1985). The relationship between nest orientation and thermal advantage is usually inferred rather than assessed directly, but particularly compelling evidence comes from species that change the orientation of nests under different climatic conditions (e.g., Ricklefs and Hainsworth 1969; Austin 1974, 1976; Facemire et al. 1990). The northern direction of prevailing winds in our study area and the evidence that vegetation does not appear to afford much protection from wind indicates that a northern orientation of nests would not ameliorate wind. An alternate explanation for nest orientation is the reduction of solar intensity. Nests of longspurs and larks are relatively exposed to solar radiation, particularly during midday, but a northern orientation of nests may still reduce solar intensity given the tracking of the sun across the southern portion of the sky during the breeding season.

Differences in relative nest exposure among species cannot be attributed ultimately to differences in egg reflectance. It might be expected that species with low egg-reflectance values would re-

quire shaded nests, but the species with the least reflective eggs in our study, the McCown's Longspur, also had the most exposed nests. As a caveat, however, our measure of egg reflectance may be incomplete because reflectance at longer wavelengths (e.g., infrared) was not measured. Thus, we can only make limited inferences regarding the potential of eggs to withstand heat stress for these three species.

THERMAL CONSTRAINTS ON NEST PLACEMENT

The contrasting strategies of nest placement between longspurs/larks and buntings may be understood by examining the potential thermal constraints of these species. There is overlap in the onset of breeding among these two groups of birds, but the delayed arrival of buntings onto the study area produces some temporal separation. Subsequently, nesting buntings generally experience higher ambient temperatures and reduced wind velocities relative to the two earlier nesting species. Buntings also exhibit biparental incubation, unlike the other two species. Because male buntings have dark plumage, radiative cover and opportunities for convective cooling are probably important in reducing heat loads for incubating males. Dark feathers may actually minimize penetration of radiative heat through the plumage if wind is present (Walsberg et al. 1978, Walsberg 1983); the increased air flow into bunting nests may therefore facilitate convective cooling. Thus, avoidance of heat stress may drive nest-site selection in Lark Buntings. This is corroborated by Pleszczynska's (1978) documentation of a correlation between radiative cover and reproductive success in Lark Buntings. The blue eggs of buntings provide additional evidence that the nesting biology of this species may have been selected to minimize heat stress; blue pigments increase the reflectance of eggs in the near-infrared, thus reducing the potential for overheating due to solar radiation (Bakken et al. 1978). Blue eggs presumably are not cryptic to visual predators, and thus the high degree to which bunting nests are associated with vegetation may additionally serve to conceal eggs.

Alternatively, longspurs and larks may experience extreme climatic conditions during the early portion of the breeding season, when incubating females are subjected to cold ambient temperatures and wind squalls. Under these conditions, the high degree of nest exposure to solar
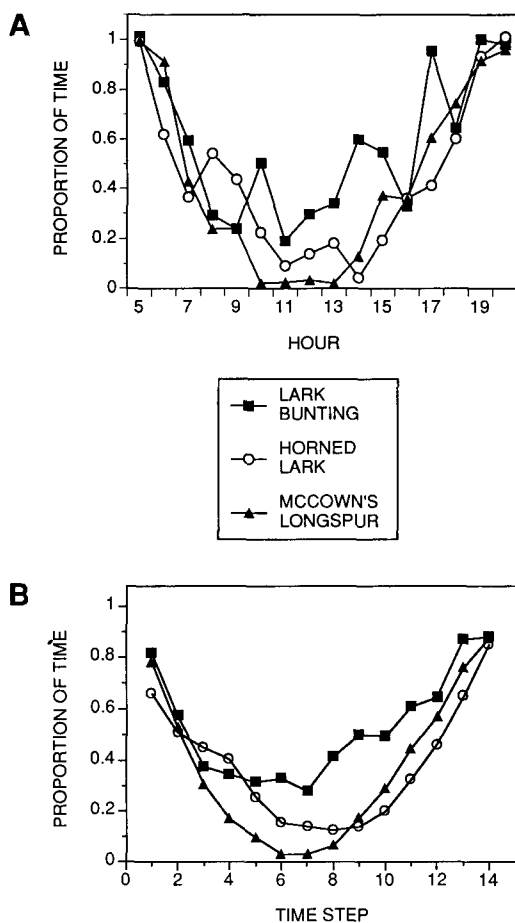

FIGURE 6.   A. Comparison of shade profiles at nests for three species of grassland birds: McCown's Longspur (n = 5 nests), Horned Lark (n = 7), and Lark Bunting (n = 5). Radiative cover of nests was assessed as the proportion of time that nests were completely shaded during one-hour time blocks throughout the day during the incubation period. B. Time-series analysis of shade profiles at nests of three grassland bird species. Analysis represents a three-step moving average (e.g., Time Step 1 is the average of the mean proportion of time that nests were shaded at 04:00, 05:00 and 06:00).

radiation may be adaptive. The protracted breeding seasons for these two species (especially McCown's Longspurs), however, would presumably subject nesting birds to a wide range of climatic conditions which also may include exposure to heat stress.

All of the nests used in this study were from the early portion of the breeding season. If avoidance of heat stress promotes nest placement by longspurs and larks in response to radiative cov-

er, then we would expect to find late-season nests associated primarily with vegetation types that afford shade, such as shrubs. Early (Julian date ≤ 161) nests of McCown's Longspurs in the MG pasture were associated mainly (59%, total n = 17) with bunch grasses (e.g., *Aristida, Bouteloua, Stipa*), whereas later nests were associated with cactus (36%) and shrubs (*Chrysothamnus, Gutierrezia*; 21%). Association of nests with these three types of vegetation, however, did not differ significantly between early and late nests (χ^2 = 5.183, df = 2, $P > 0.05$; Chi-square Analysis). Association of nests with a particular vegetation type may instead reflect phenological differences in substrate availability. In the HG pasture, which is floristically and structurally simpler than the MG pasture, longspur nests were usually placed beside cactus (early nests = 49%, late nests = 63%), and there was no significant difference in nest association with the three types of vegetation throughout the season (χ^2 = 1.472, df = 2, $P \geq 0.05$; Chi-square Analysis). Additionally, longspurs did not orient their nests differently with respect to vegetation at different times in the season (F = 1.47, df = 1,76, $P > 0.05$; Watson-Williams Test).

If vegetation does not serve to ameliorate the microclimate of longspur and lark nests, then why are nests associated with vegetation or other structural features of the prairie? Association with vegetation may have other functions including diffusion of predation risk (e.g., Martin and Roper 1988) or to provide "cues" to nest location (but see Maclean and Moran 1965). Most nest failures in this system are attributable to predation, resulting in low reproductive success for all three species (Strong and Ryder 1971). Working with Mountain Plovers (*Charadrius montanus*) in the same area as our study, Graul (1975) explained the association of nests with cow pats as providing a "disruptive effect" that concealed nests from predators. Further, the cryptic coloration of longspur and lark eggs suggests that predation may have influenced selection for egg pigmentation in these two species, as opposed to the unpatterned eggs of buntings. It is plausible, therefore, that nest-site selection in larks and longspurs may be based primarily on an antipredation strategy rather than a biophysical one. Indeed, nest-site selection undoubtedly represents a trade-off between a number of competing constraints. Quantification of these constraints is necessary to establish the relative importance of different factors in dictating nest placement.

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