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ORIENTATION AND MICROCLIMATE OF HORNED LARK NESTS: THE IMPORTANCE OF SHADE

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Abstract. Across their range, Horned Larks (*Eremophila alpestris*) consistently construct their nests ad-

acent to and north of a conspicuous object such as a tuft of grass, shrub, or rock. We studied the relative importance of a northern nest orientation to nest microclimate in Horned Larks breeding in northeastern California. Nests showed a significant northern bias in orientation angle and were 49% shaded in the early afternoon, the hottest part of the day. Artificial nests

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of eastern, western, and southern orientations exhibited little to no shade during this time. A northern nest orientation also allowed nests to face prevailing winds during the day and avoid them in the evening. The Horned Larks' preference for a northern nest orientation offers multiple advantages for regulation of nest microclimate.

Key words: *Eremophila alpestris*, *Horned Lark*, *microclimate*, *nest entrance*, *nest orientation*, *shade*, *solar radiation*.

Orientación y Microclima en Nidos de *Eremophila alpestris*: La Importancia de la Sombra

Resumen. De forma consistente a lo largo de su rango de distribución, *Eremophila alpestris* construye sus nidos adyacentes a y al norte de objetos conspicuos, como parches de pasto, arbustos o rocas. Estudiamos la importancia relativa de la orientación de los nidos hacia el norte para el microclima de éstos en individuos de *E. alpestris* que se reproducen en el noroeste de California. El ángulo de orientación de los nidos presentó un sesgo significativo hacia el norte y éstos tuvieron un 49% de sombra durante las primeras horas de la tarde, el período más caliente del día. Nidos artificiales con orientación hacia el este, oeste y sur exhibieron poca o ninguna sombra durante esa parte del día. La orientación hacia el norte también permitió a los nidos orientarse hacia la dirección predominante del viento durante el día y evitar los vientos durante el atardecer. La preferencia de *E. alpestris* por la orientación de los nidos hacia el norte ofrece múltiples ventajas para la regulación del microclima del nido.

The regulation of nest microclimate is especially important to birds breeding in harsh environments and for species with low tolerance to fluctuations in nest microclimate (Ricklefs and Hainsworth 1969, Calder 1973, Austin 1974, 1976, McGillivray 1981, Walsberg 1981). Amelioration of adverse environmental conditions on eggs, young, and incubating adults can greatly improve reproductive success (Walsberg and King 1978, Webb and King 1983, Walsberg 1985). Accordingly, many birds have developed specific nesting characteristics that allow them to regulate nest microclimate. Several woodpeckers and other cavity nesters exhibit significant directional bias in nest entrance orientation, associated with avoiding or facing prevailing winds and maximizing or minimizing solar radiation within the nest (Connor 1975, Crockett and Hadow 1975, Austin 1976, Inouye 1976, Inouye et al. 1981, Vinuela and Sunyer 1992). Cactus Wrens (*Campylorhynchus brunneicapillus*) orient their nest entrance away from prevailing winds in the early, cooler part of the breeding season yet toward the wind during the hot summer (Ricklefs and Hainsworth 1969). Cactus Wren nest orientation also appears to reduce solar radiation within the nest (Facemire et al. 1990).

Although less studied, a few open-cup nesters also exhibit specific nest entrance orientations relative to surrounding biotic or abiotic material (Cannings and Threlfall 1981, Finch 1983, With and Webb 1993). The

Horned Lark (*Eremophila alpestris*) is a small ground-nesting passerine that breeds throughout North America in open habitats containing sparse vegetation and bare soil. Females typically build nests directly adjacent to an object such as a tuft of grass, small shrub, rock, or dirt mound. (Beason and Franks 1974, Cannings 1981, Cannings and Threlfall 1981). Previous studies suggest that Horned Larks orient their nests next to objects to block prevailing winds or to shade nests from solar radiation. In Cape St. Mary's, Newfoundland, Horned Lark nests exhibited western to northeastern orientations ($n = 15$; Cannings and Threlfall 1981), which may have afforded protection from prevailing winds that were primarily from the southwest. In north-central Colorado, Horned Lark nests exhibited a significantly northeastern orientation ($n = 10$; With and Webb 1993), yet prevailing winds were from the northwest and southeast, making a windbreak an unlikely function. However, these same nests were completely shaded for 45% of the day, providing support to the idea that Horned Lark nest orientation is a means of reducing solar radiation within the nest (With and Webb 1993).

Climatic differences across a species' breeding range can complicate the study of nest-site selection. The direction of wind and solar radiation often coincide making it difficult to discern which aspect(s) influences selection of a specific nest-site. In addition, nonclimatic factors such as risk of nest predation can alter nest-site selection. Observational studies do not allow comparison to nests of different orientation, as often all natural nests share a common orientation. Here we compare solar radiation and protection from wind among naturally used, northerly oriented Horned Lark nests in northeastern California and nearby artificial nests having the same and different compass orientations.

METHODS

STUDY AREA

This study was conducted in the spring and summer of 2001 at the Jay Dow Sr. Wetlands. Jay Dow Sr. Wetlands is a 540-ha constructed wetland located at the southern end of Honey Lake in Lassen County, California (40°7'N, 120°14'W, elevation 1220 m). Sixteen fresh to brackish ponds encompassing 130 ha provide habitat for thousands of breeding and migrating waterbirds. The remaining area is composed of salt desert scrub dominated by annual grasses, primarily cheatgrass (*Bromus tectorum*), perennial grasses (saltgrass [*Distichlis spicata*], Great Basin wildrye [*Elymus cinereus*], squirreltail [*Sitanion hystrix*], and Indian ricegrass [*Oryzopsis hymenoides*]) and shrubs (greasewood [*Sarcobatus vermiculatus*], sagebrush [*Artemisia tridentata*], and gray rabbitbrush [*Chrysothamnus nauseosus*]).

The climate of the Honey Lake Basin is typical of the western Great Basin, with cool, wet winters and hot, dry summers. In the summer, winds are primarily from the north to northeast.

DATA COLLECTION

We located 10 Horned Lark nests between 9 May and 15 June 2001. Each nest was situated adjacent to a

conspicuous tuft of grass; five adjacent to grass tufts taller than the surrounding vegetation ($n = 3$ squirrel-tail and $n = 2$ Indian ricegrass), and five next to tufts of the much shorter and more common saltgrass. At each nest we measured nest orientation, nest depth and diameter, and the structure of the adjacent grass tuft. We defined nest orientation as the angle bisecting the entrance to the nest. The nest entrance is the area around the nest without the typical protective structure of vegetation and is the direction by which incubating birds leave from and return to the nest.

We examined differences in daily temperatures and degree of shading as a function of nest orientation on six natural nests. We selected six nests so that each round of data collection could be completed within 2 hr. As all Horned Lark nests were oriented in a northerly direction (320° to 40°), we were unable to examine differences in temperature or degree of shading among orientations across a 360° plane. Thus, for each natural nest we constructed artificial nests of eastern (orientation + 90° of natural), southern (orientation + 180° of natural), and western (orientation - 90° of natural) orientations. We also constructed nests of the same orientations as the natural nests and "open" orientations, which consisted of depressions similar to natural nests but devoid of any significant surrounding vegetation. Thus, for each of six natural Horned Lark nests, we constructed artificial nests of east, south, west, north, and open orientations for a total of 36 nests (six of each orientation plus six natural nests). Each artificial nest was constructed using available grass tufts within 3 m of the corresponding natural nest and matched with natural nests for depth, diameter, and vegetation height, width and structure. To insure that grass tufts of artificial nests were representative of the grass tuft of the corresponding natural nest, height and width measurements were taken at 5-cm intervals both horizontally and vertically at each Horned Lark nest. These data allowed us to construct approximate copies of the three-dimensional structure of the grass tufts of natural nests, by either trimming or adding vegetation to grass tufts of artificial nests.

Three times daily we recorded temperature and the percent shade present in all nests, once in the morning (08:00–10:00), early afternoon (12:00–14:00), and late afternoon (16:00–18:00), from 30 June to 8 July 2001 (total of six days, $n = 18$ samples per nest). So as not to interfere with nesting Horned Larks, we waited until all nests were vacated prior to conducting this study. We estimated the amount of shade in each nest by placing a sheet of graph paper of the same dimensions as the nest cup into each nest and then counting the number of squares shaded during each observation. By dividing the number of shaded squares by the number of total squares we calculated percent shading of each nest. We recorded nest temperature by centering a Thermistor Thermometer Model 8402-00 (Cole-Parmer Instrument Company, Vernon Hills, Illinois) approximately 1 cm above the nest floor.

We determined mean wind direction over the duration of the Horned Lark's nesting season (01 April–30 July 2001) by averaging hourly records taken from the RAWS weather station in Doyle, California ($40^\circ 1' N$, $120^\circ 6' W$, elevation 1290 m), approximately 15 km

southwest of the Jay Dow Sr. Wetlands. Both sites are in the Honey Lake Valley and share common weather patterns.

STATISTICAL ANALYSES

We used Rayleigh's test (Zar 1999) to assess whether nest orientation of the 10 original Horned Lark nests was randomly distributed around 360° . Where nest orientation distribution was found to be nonrandom, we used a one-sample test with 95% confidence limits to test the hypothesis of a northern orientation (Zar 1999).

We used regression analysis on all measured nest characteristics (depth, diameter, vegetation height, vegetation width) to determine if any of these variables significantly predicted nest orientation (i.e., natural, north, west, south, east). Differences among orientations in degree of shading and nest temperature were assessed using repeated measures ANOVA. Multiple comparisons between treatment means were performed using Tukey's test. Results are reported as means \pm SE unless otherwise indicated. All statistical tests were performed using SAS (SAS Institute Inc. 1988) and were considered significant at $P < 0.05$.

RESULTS

NEST ORIENTATION

Horned Larks oriented their nests nonrandomly relative to adjacent grass tufts ($\chi = 8.0$, $n = 10$, $P < 0.001$). Horned Lark nests displayed a significant north by northwest orientation (one-sample test: mean \pm 95% CI = $345 \pm 20^\circ$).

WIND DIRECTION

Prevailing winds were from the northeast during the day (06:00–18:00, mean \pm 95% CI = $51 \pm 18^\circ$), and from the south at night (18:00–06:00, mean \pm 95% CI = $168 \pm 9^\circ$). The range in position of the vegetation around nests was from 50° to 270° . Thus, nests were exposed to winds throughout the day and protected from them in the evening (Fig. 1).

SOLAR RADIATION

None of the measured nest characteristics significantly predicted nest orientation ($P > 0.9$). Percent shading varied among orientations ($F_{5,30} = 18.5$, $P < 0.001$; ANOVA). In the early afternoon, northerly oriented nests were significantly more shaded than all other orientations (Table 1). No other orientation averaged more than 9% shading at this time of day. Likewise, in late afternoon, nests with northern orientations were significantly more shaded than all other orientations with the exception of easterly oriented nests (Table 1).

NEST TEMPERATURE

Although some of the same trends were present in the temperature analysis, few significant differences were found between treatments. Northerly oriented nests were significantly warmer in the morning than southerly or westerly oriented nests (Table 1). In the early afternoon, nests with northern orientations averaged the coolest of all orientations, but differed statistically only from easterly oriented nests (Table 1).

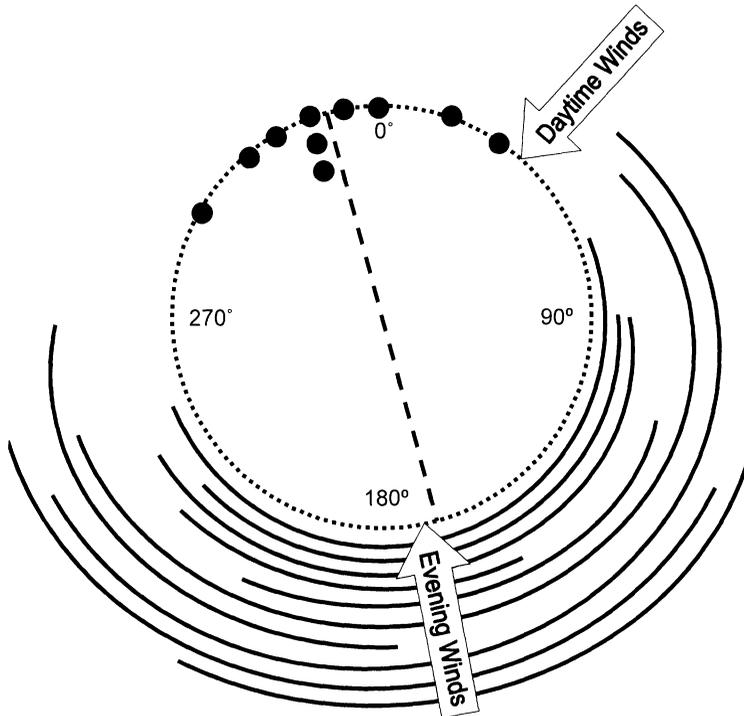


FIGURE 1. The position of vegetation (curved black bars) around Horned Lark nests at the Jay Dow Sr. Wetlands, California, relative to the directional heading of prevailing winds. The dashed circle represents the outline of a nest. Each individual curved black bar represents the vegetation around one nest. Each solid circle represents one entrance orientation. The dashed line designates the mean entrance orientation angle of 345° for all nests ($n = 10$).

DISCUSSION

Horned Larks breeding at the Jay Dow Sr. Wetlands orient their nests in a north by northwest direction, a behavior that minimizes solar radiation within the nest. The amount of shade within individual Horned Lark nests averaged 49% or greater throughout the day. The ability for an open-ground nesting bird to achieve this using a small tuft of grass is remarkable. The Horned Lark's preference for northerly oriented nest-sites ensures maximal shading by the grass tuft to the south.

A northern orientation may also protect nests from evening winds. In the evening, winds were primarily from the south, and all grass tufts were positioned from southwest to east of nests. Thus, a northern nest orientation may allow Horned Larks to reduce exposure to cooling winds during the night. Conversely, a northern nest orientation may provide increased daytime ventilation of the nest through exposure to prevailing winds, a situation that may prove equally beneficial in the hot, arid climate of the Great Basin.

In addition to the potential microclimatic benefits associated with a northern nest orientation, shade may also conceal nests from predators. In the mid- to late afternoon the amount of shade within Horned Lark nests was often so extensive that eggs or nestlings might have been more difficult for predators to detect, therefore decreasing the probability of nest predation.

Because multiple factors influence the nest success of birds (e.g., regulation of nest microclimate, predation risk), finding conclusive evidence for the adaptive significance of nest placement can be difficult. In addition, the relative benefits of a specific nest placement may be missed through purely observational studies dealing with natural nests. In this study, comparison among artificial nests showed that those with northern orientations were 31% shaded in the early afternoon, significantly more than any other orientation. As it is common knowledge that the sun moves across the southern sky in the northern hemisphere, we would predict *a priori* that nests with northerly orientations would receive more shade than nests with other orientations. The purpose of this experiment was not to determine which nest orientation afforded the most microclimatic benefit, but rather to demonstrate the relative benefit afforded by a northern orientation versus an alternate orientation. In previous studies, authors have been hesitant to conclude that Horned Larks select a northern nest orientation to maximize nest shade because nests were not greatly shaded during the hot afternoon (With and Webb 1993). While 31% shading of the nest may not seem like a large amount in absolute terms, in relative terms it is immense. In this study, no other nest orientation yielded more than 9%

TABLE 1. Mean \pm SE percent shade and temperature of six natural Horned Lark nests and artificial nests of north, south, east, west, and open orientations (six nests per orientation) relative to adjacent grass tufts. Shade and temperature were measured within three time periods (morning 08:00–10:00, early afternoon 12:00–14:00, and late afternoon 16:00–18:00). "A" denotes a significant difference from natural nests (Tukey's test); "B" denotes a significant difference from artificial nests of northern orientation.

Time of day	Orientation					
	North (natural)	North (artificial)	South	East	West	Open
% Shade						
Morning	60 \pm 4	22 \pm 4 A	61 \pm 4 B	9 \pm 4 AB	86 \pm 4 AB	6 \pm 4 AB
Early afternoon	49 \pm 4	31 \pm 4	1 \pm 4 AB	6 \pm 4 AB	9 \pm 4 AB	0 \pm 4 AB
Late afternoon	76 \pm 4	58 \pm 4 A	17 \pm 4 AB	94 \pm 4 AB	10 \pm 4 AB	9 \pm 4 AB
Temperature (°C)						
Morning	35.8 \pm 1.0	34.9 \pm 1.0	29.6 \pm 1.0 AB	36.4 \pm 1.0	28.3 \pm 1.0 AB	34.7 \pm 1.0
Early afternoon	45.7 \pm 1.0	45.6 \pm 1.0	50.1 \pm 1.0	51.2 \pm 1.0 AB	47.6 \pm 1.0	49.0 \pm 1.0
Late afternoon	41.2 \pm 1.0	41.2 \pm 1.0	44.2 \pm 1.0	37.9 \pm 1.0	42.3 \pm 1.0	42.6 \pm 1.0

shade in the early afternoon, the hottest time of the day.

Although northerly oriented nests exhibited significantly more shade than all other nest orientations, these same nests were not significantly cooler. Only one temperature reading was recorded at each nest per time period per day, so it is likely that wind gusts, especially in the late afternoon, accounted for the large variation in temperature measurements within nests. Although we tried to record temperatures only when the wind was calm, we could not always do this if all data were to be collected within a 2-hr period. A more accurate representation may be achieved by using data-loggers to record temperatures constantly throughout the day.

The Horned Lark's preference for a northern nest orientation from California to Colorado to Newfoundland provides support to the hypothesis that nest orientation is selected to ensure maximal shading of the nest. In these three locations the direction of prevailing winds was different, yet nest orientations were similar. Conversely, the movement of the sun across the sky is virtually identical at all three locations, thus providing equal stimulus to which these birds react. Interestingly, six species of lark (Alaudidae) breeding in the Kalahari sandveld of southern Africa also exhibited directional biases in nest orientation associated with increased nest shade (Maclean 1970). In contrast to North American Horned Lark nests, however, nests of these species were predominantly oriented to the southeast. As these species nest in the southern hemisphere where the sun moves across the northern sky, we would predict a southern nest orientation to afford the most nest shade.

A northern nest orientation offers multiple potential benefits to nesting Horned Larks. The fact that several lark species nesting in the southern hemisphere exhibit an approximately 180° reversal in nest orientation leads us to believe that many lark species have adapted specific nest orientations in response to the position and movement of the sun. Whether larks do this to regulate nest microclimate or to reduce predation risk remains to be decided, yet the hot and arid nature of their breeding environments makes microclimate a likely candidate.

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