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THERMAL ASPECTS OF NEST-SITE LOCATION FOR VESPER SPARROWS AND HORNED LARKS IN BRITISH COLUMBIA

KARI J. NELSON AND KATHY MARTIN

Abstract. During the 1994 and 1995 breeding seasons, we examined the orientation of Vesper Sparrow (*Pooecetes gramineus*) and Horned Lark (*Eremophila alpestris*) nests relative to vegetative cover in the Chilcotin grasslands of central British Columbia. To investigate the effects of nest placement on nest microclimate, we compared nest temperatures with (1) different orientations relative to single clumps of vegetative cover, (2) different orientations relative to multiple clumps of vegetative cover, and (3) different amounts of vegetative cover. Vegetation was located on the southwest side (180–260°) of 87 percent of nests of both species. The distribution of single clumps of vegetation (77 percent of nests) around nests of both species in both years differed significantly from a uniform distribution. Nests with either a single clump of vegetation on the southwest side or with more than one clump of vegetation on the southeast to southwest side had lower temperatures than did nests with vegetation on other sides; these nests also remained above the temperature that may be lethal to developing embryos (38 C) for shorter periods of time during the day than did other nests. Nests without vegetation on the east side warmed up more rapidly in the morning than did nests with vegetation on the northeast or southeast side. The height of the vegetation clump and the amount of cover it provided also influenced nest temperatures. Nests with more than 90 percent cover exceeded 38 C for only 1.25 hours at midday, whereas nests with less than 20 percent cover exceeded 38 C for 4.25 hours. The pattern of nest orientation displayed by Vesper Sparrows and Horned Larks in this study appeared to reflect selection for thermally advantageous nest sites.

LOS ASPECTOS TÉRMICOS DE LA UBICACIÓN DE NIDOS PARA LOS GORRIONES COLIBLANCOS Y LAS ALONDRAS CORNUDAS EN COLOMBIA BRITÁNICA

Sinopsis. Durante las temporadas reproductivas de 1994 y 1995, examinamos la orientación de los nidos del Gorrión Coliblanco (*Pooecetes gramineus*) y de la Alondra Cornuda (*Eremophila alpestris*) con relación a la cobertura vegetativa en los pastizales Chilcotin del centro de Colombia Británica, Canadá. Para investigar los efectos de la colocación de nidos en el microclima, comparamos las temperaturas de los nidos con (1) diferentes orientaciones con relación a matas sencillas de cobertura vegetativa, (2) diferentes orientaciones con relación a matas múltiples de cobertura vegetativa, y (3) diferentes cantidades de cobertura vegetativa. La vegetación se ubicaba al lado suroeste (180–260°) en un 87 por ciento de los nidos de ambas especies. La distribución de las matas sencillas de vegetación (un 77 por ciento de los nidos) alrededor de los nidos de ambas especies en los dos años difirió significativamente de una distribución uniforme. Los nidos que tenían o una mata sencilla al lado suroeste o más de una mata de vegetación al lado sureste a suroeste registraron temperaturas más bajas que los nidos con vegetación a los otros lados; estos nidos también tenían temperaturas más altas que la temperatura que puede ser mortal para los embriones en desarrollo (38 C) durante temporadas más cortas en el transcurso del día en comparación con la temporada que tenían los otros nidos. Los nidos que no tenían vegetación al lado este se calentaron más rápidamente en la mañana que los nidos con vegetación al lado noreste o sureste. La altura de la mata de vegetación y la cantidad de cobertura que ofrecía también influyeron en las temperaturas de los nidos. Los nidos que tenían cobertura de más de un 90 por ciento sobrepasaron los 38 C solamente por 1,25 horas alrededor del mediodía, mientras que los nidos con cobertura de menos de un 20 por ciento sobrepasaron los 38 C durante 4,25 horas. La tendencia en la orientación de los nidos que mostraron los Gorriones Coliblancos y las Alondras Cornudas en este estudio pareció reflejar una selección de sitios de nidos con ventajas térmicas.

Key Words: British Columbia; grassland birds; habitat selection; microclimate; nest placement; vegetative cover.

Choosing an appropriate nest site plays a critical role in the reproductive success of birds. Nest placement may influence the ability of predators to detect nests (Martin 1993) and the degree to which nests are sheltered from extreme environmental conditions (Walsberg 1985). Grassland environments are characterized by extreme environmental conditions, including intense solar radiation. Microclimatic conditions therefore may be a particularly important aspect of nest-site selection for open-nesting species in grassland habitats.

Studies of a wide variety of bird species have attributed nonrandom patterns of nest placement with respect to vegetative cover to protection from wind or solar radiation (Ricklefs and

Hainsworth 1969, Orr 1970, Austin 1976, Cannings 1981, Cannings and Threlfall 1981, Verbeek 1981, Zerba and Morton 1983a, Facemire et al. 1990, Petersen and Best 1991). Few of these studies, however, have documented the influence of nest orientation on nest microclimate (but see With and Webb 1993). Our study is part of an ongoing investigation into thermal aspects of nest placement of Horned Larks (*Eremophila alpestris*) and Vesper Sparrows (*Pooecetes gramineus*) in the Chilcotin grasslands of British Columbia. In this paper we test the hypothesis that these species orient their nests nonrandomly with respect to vegetative cover. To illustrate the effects of nest-site selection on nest microclimate, we compare nest temperatures obtained from nests with (1) different orientations relative to single clumps of vegetative cover, (2) different orientations relative to multiple clumps of vegetative cover, and (3) different amounts of vegetative cover.

STUDY SITES

Field work was conducted during the 1994 and 1995 breeding seasons at Becher's Prairie near Riske Creek, British Columbia (51°58′ N, 122°32′ W). Becher's Prairie has an elevation of approximately 1,000 m and consists of grassland habitats interspersed with small lakes and copses (trembling aspen [*Populus tremuloides*], Douglas-fir [*Pseudotsuga menziesii*], and lodgepole pine [*Pinus contorta*]). The dominant vegetation in the area is bluebunch wheatgrass (*Elymus spicata*), June grass (*Koeleria macrantha*), porcupine grass (*Stipa curtiseta*), and Kentucky bluegrass (*Poa pratensis*).

We sampled six sites ranging in size from 36 to 74 ha and comprising a total of 364 ha. Grazing by domestic cattle has occurred on most grasslands in the system, and fire is presently being reintroduced as a range-management tool to reduce forest encroachment and enhance forage production. Vesper Sparrows and Horned Larks are the most common breeding passerines in the area.

METHODS

We located Horned Lark and Vesper Sparrow nests by flushing females from nests while walking through the study sites or by rope-dragging (Labisky 1957). The majority of nests of both species were located immediately adjacent to (i.e., touching) the base of perennial bunchgrasses (porcupine grass or bluebunch wheatgrass; K. Nelson, unpubl. data). Individual plants of these species form discrete, densely tufted clumps of vegetation. After a nest was vacated, we determined the orientation (relative to true north) of any clumps of vegetation (i.e., individual plants) touching it by measuring the compass direction of a line bisecting the center of the nest and the center of the vegetation clump(s). In the few cases (N = 10) where a nest was completely surrounded by vegetation, we did not measure the orientation of individual clumps.

Calculations of descriptive statistics and significance tests for data from circular distributions (i.e., orientation of vegetation relative to nests) followed Zar 1984. Differences between mean angles of orientation of vegetation relative to nests were determined using the Watson-Williams test, and Rayleigh's test was used to determine whether the distribution of vegetation around nests was uniform.

We quantified the amount of nest concealment using a 6.5-cm-diam ball marked with a grid of 61 dots (2 mm diam). The dots were drawn on the ball so they would appear equidistant (8 mm apart) when viewed from a distance of 1 m. This ball fit snugly into the nest cups of both species, thus providing an objective, readily repeatable method of measuring nest concealment. Overhead cover was determined by placing the ball in the nest cup with the grid axes oriented along each of the four cardinal compass directions. The number of dots visible from a height of 1 m above the nest was counted, and the proportion of the nest concealed was calculated by dividing the number of dots not visible by the total number of dots. We also measured the maximum height of the vegetation clump(s) adjoining the nest.

In 1995 we measured nest temperatures by placing a single HOBO™ data logger (temperature range −37 to +46 C) inside nest cups as soon as possible after they were vacated. Nest temperatures were recorded every 5–6 min over a 6- or 8-d period. A maximum of 13 nests could be monitored at one time, so data were collected over six separate time periods during the summer. In total, we recorded temperature profiles for 49 Vesper Sparrow nests and 16 Horned Lark nests.

In this paper we present temperature data from nests with single clumps of vegetation on the southwest, northwest, northeast, or southeast side; with multiple vegetation clumps on different sides; and with different amounts of vegetative cover. To control as much as possible for the effects of weather, we present nest temperatures obtained only on clear days, and we limit direct comparisons to data collected on the same day. To facilitate comparisons between nests, the temperature presumed lethal for embryos (38 C; Zerba and Morton 1983b) appears on all plots of nest temperatures. To provide an indication of the range of temperatures potentially experienced by birds and nests in this system, we also present temperature data recorded by a HOBO data logger that was placed on the ground in an exposed location on a clear day.

RESULTS

NEST ORIENTATION

We located a total of 122 nests in 1994 and 1995: 19 Horned Lark and 103 Vesper Sparrow. We found 77% of nests of both species (17 Horned Lark, 77 Vesper Sparrow) at the base of a single clump of vegetation. For these nests, there was no significant difference between years in the mean angle of orientation of vegetation relative to nests of either species (Horned Lark: $F_{1,16} = 3.27$, $P > 0.05$; Vesper Sparrow: $F_{1,76} = 2.69$, $P > 0.10$). There was also no significant difference between species in the mean angle of orientation of vegetation relative to nests for both years combined ($F_{1,93} = 0.43$, $P > 0.25$). The distribution of single clumps of

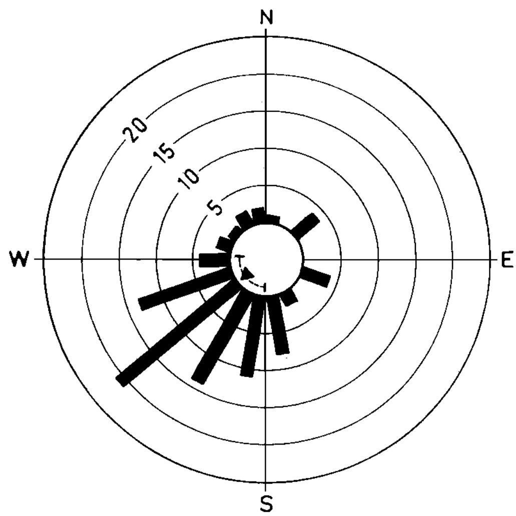

FIGURE 1. Frequency distribution of the orientation of single clumps of vegetation relative to Vesper Sparrow and Horned Lark nests (center of figure). N represents true north, the triangle represents the mean angle of orientation of vegetation relative to nests, and the dashed lines represent the angular deviation.

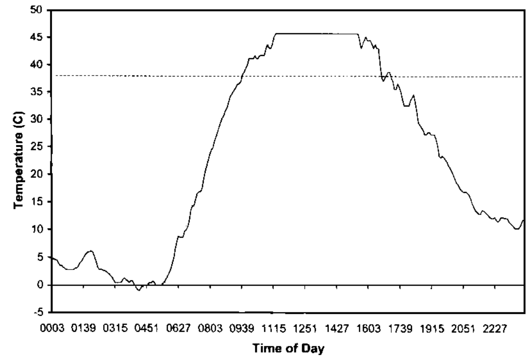

FIGURE 2. Temperature profile from a HOBO data logger placed in an exposed location on the ground on a clear day (3 June 1995). The dotted horizontal line (38 C) represents the presumed lethal temperature for embryos.

vegetation around nests of both species in both years was significantly nonuniform (mean angle = 230.4°, s = 33.6°, z_{94} = 40.09, $P < 0.001$; Fig. 1).

We found 23% of nests (2 Horned Lark, 26 Vesper Sparrow) adjoining more than one clump of vegetation. Ten of these nests were completely surrounded by vegetation, and one was under a branch. The other 17 nests with multiple clumps of vegetation all had one clump of vegetation on the southwest side of the nest.

Temperature Profiles

Temperatures recorded in an exposed location on the ground on 3 June 1995 ranged from below 0 C before dawn to 45.7 C (the maximum recordable temperature on the HOBO data logger) at midday (Fig. 2). For more than 7 hr between 0942 and 1647, the temperature exceeded 38 C. During this time, eggs exposed to the sun would rapidly have exceeded temperatures presumed lethal for embryos (Zerba and Morton 1983b), and adults incubating eggs or sheltering young would have needed to expend energy cooling themselves and their eggs or young (Grant 1982). Although we collected temperature data in an exposed location on only one day, the results clearly demonstrate the temperature extremes to which birds and nests in this area may be exposed. In all cases where maximum temperatures were recorded, actual temperatures were probably at least 10 degrees higher.

Nest temperatures differ depending on how long and during what time of day nests are exposed to solar radiation. To examine the influence of nest orientation relative to vegetative cover on nest temperatures, we selected nests that were as similar as possible with respect to height of vegetation beside the nest and amount of nest concealment (Table 1). We collected temperature data for only one nest with vegetation on the northeast side and one nest with vegetation on the northwest side (because nests with these orientations were rare). We compared temperatures from these nests to temperatures obtained on the same day from nests with vegetation on the opposite sides of the nest (southwest and southeast sides, respectively).

On 15 June 1995, temperatures in the nest with vegetation on the southwest side (N5) rose much more rapidly in the morning than did temperatures in the nest with vegetation on the northeast side (KN2; Fig. 3A). Temperatures in N5 reached a peak of 30.2 C in 4.5 hr, at 1008. Temperatures in KN2 did not surpass 30.2 C until 1147 (6.25 hr after warming began) and rose gradually to the maximum recordable temperature of 45.7 C between 1417 and 1502. Temperatures in KN2 were above 38 C for less than 3 hr (from 1307 to 1553).

Temperatures in nests with vegetation on the northwest side (N31) and southeast side (N23) were recorded later in the season, on 19 July 1995 (Fig. 3B). Temperatures in these nests were approximately 5 degrees higher at 2400 than they were in nests with vegetation on the southwest and northeast sides (Fig. 3A). Temperatures rose more rapidly in N31 than in N23, surpassing 38 C by 1040 (4.75 hr after the nest began to heat up) and remained above this temperature for 6 hr (until 1645). Temperatures in N31

TABLE 1. ORIENTATION OF VEGETATION RELATIVE TO NESTS (COMPASS DIRECTION), HEIGHT OF VEGETATION, AND AMOUNT OF VEGETATIVE COVER FOR EACH OF THE NESTS USED IN COMPARISONS OF NEST TEMPERATURES

Comparison	Nest	Species[a]	Compass direction	Height (cm)	% nest cover
Orientation of single clumps (Fig. 3)	KN2	VESP	56°	41	77
	N5	VESP	227°	33	58.4
	N23	VESP	117°	27.5	42.6
	N31	VESP	318°	32	63.9
Orientation of multiple clumps (Fig. 4)	KN7	VESP	84/169/238°	33/35/31	63.9
	KN3	VESP	128/236°	21.5/33	37.7
	N4	VESP	211/297°	32.5/35	91.8
	N6	VESP	168/236/310°	37/33/34	98.4
Size of clump (Fig. 5)	KN13	HOLA	225°	16	18
	N1	VESP	222°	33	39.3
	RN3	VESP	219°	57	90.2

[a] VESP = Vesper Sparrow, HOLA = Horned Lark.

reached the maximum recordable temperature (45.7 C) at 1118 and dropped below this temperature at 1521. Temperatures in N23 did not surpass 38 C until 1254 (>2 hr later than in N31), reached the maximum recordable temperature at 1430, and dropped below 38 C at the same time as in N31 (1645). Both of these nests cooled at similar rates.

The effect of orientation of multiple clumps of vegetation on nest temperatures was recorded on 15 and 28 June 1995 and is illustrated in Fig. 4. Nest KN7 had vegetation on the east, south, and southwest sides, whereas KN3 had vegetation on the southeast and southwest sides. These

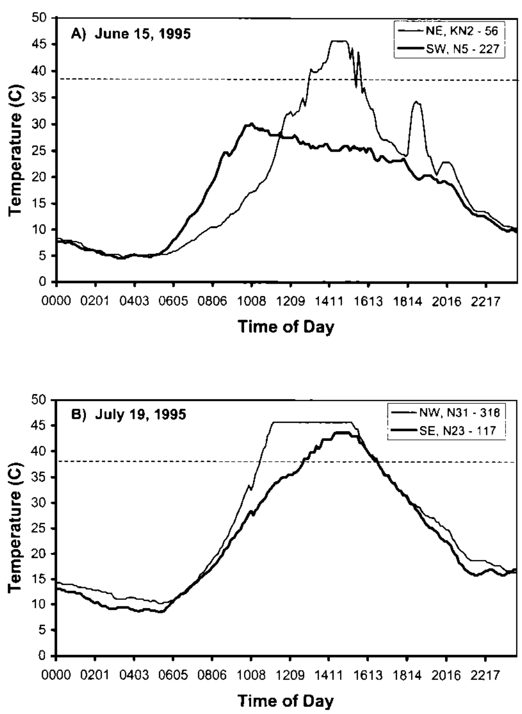

FIGURE 3. Temperature profiles for nests with a single clump of vegetation on (A) the southwest or northeast side and (B) the northwest or southeast side. The dotted horizontal line (38 C) represents the presumed lethal temperature for embryos. Numbers following nest identification codes are compass orientation (in degrees) of vegetation relative to nests.

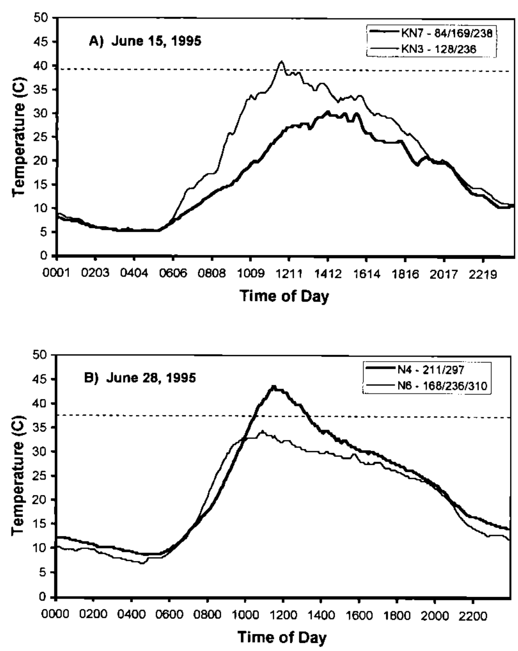

FIGURE 4. Temperature profiles for nests surrounded by more than one clump of vegetation; all nests have vegetation on the southwest side. The dotted horizontal line (38 C) represents the presumed lethal temperature for embryos. Numbers following nest identification codes are compass orientation (in degrees) of vegetation relative to nests.

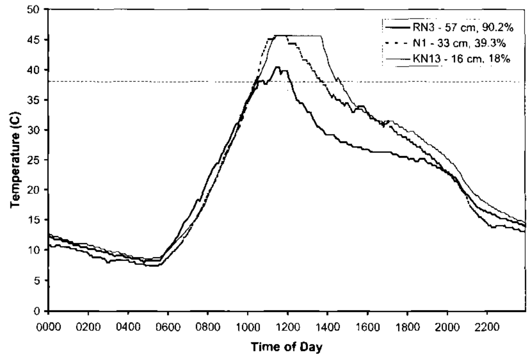

FIGURE 5. Temperature profiles recorded on 28 June 1995 for nests with different amounts of vegetative cover; all nests have vegetation on the southwest side. The dotted horizontal line (38 C) represents the presumed lethal temperature for embryos. Numbers following nest identification codes are height of vegetation and percentage of vegetative cover for each nest.

differences were reflected in a more rapid rise in temperatures in KN3 than in KN7, with temperatures in KN3 reaching a peak of 41.1 C at 1145, which was 5.75 hr after temperatures began to rise (Fig. 4A). Temperatures in KN7 peaked at a much lower temperature (30.6 C) 2.5 hr later (at 1412). Temperatures in KN3 remained above 38 C for just over 1 hr at midday (from 1126 to 1249).

Rapid increases in morning temperatures were displayed on 28 June 1995 by two nests (N4 and N6) with no vegetation on their northeast, east, or southeast sides (Fig. 4B). These nests heated at similar rates, but temperatures in N6 peaked at 34.5 C at 1053, whereas temperatures in N4 continued to rise, peaking at 43.7 C at 1126. Temperatures in N4 remained above 38 C for 2.75 hr (from 1033 to 1317). The difference in temperature profiles for these two nests is explained by the presence of an additional clump of vegetation on the south side of N6.

To examine how the amount of cover influenced nest microclimate, we compared temperature data from three nests that all had vegetation on the southwest side but that differed with respect to height of vegetative cover and amount of nest concealment (Table 1, Fig. 5). All three nests heated at similar rates on the morning of 28 June 1995. The nest with the largest clump of vegetation and the most cover (RN3) remained above 38 C for only 1.75 hr and reached a lower maximum temperature (40.5 C) than did the other two nests (N1 and KN13). N1 and KN13 reached the maximum recordable temperatures (45.7 C) by 1125, but KN13, which had the least vegetative cover, remained at this temperature for a longer period of time (2.25 hr compared with 0.5 hr for N1). Temperatures in KN13 also remained above 38 C for the longest period during the hottest time of the day.

DISCUSSION

During the breeding season, grassland environments, particularly at northern latitudes, are characterized by extreme environmental conditions, including cold nights and hot days. Most of the heat transfer between eggs or nestlings in open-nesting species occurs through convection and short-wave radiation (Webb and King 1983). In grasslands, two of the most important aspects of nest-site location should thus be protection from wind and protection from solar radiation (With and Webb 1993).

The pattern of nest orientation relative to vegetative cover displayed by Vesper Sparrows and Horned Larks in our study was similar to that reported for several other open-nesting species in a variety of ecosystems (Cannings 1981; Cannings and Threlfall 1981; Verbeek 1981; Walsberg 1981; Zerba and Morton 1983a; Petersen and Best 1985, 1991; With and Webb 1993). In some of these ecosystems, prevailing winds are from the southwest, and the observed pattern of nest orientation has been attributed either to protection from wind (Cannings 1981, Cannings and Threlfall 1981) or to protection from wind and/or afternoon sun (Zerba and Morton 1983a, Petersen and Best 1985). With and Webb (1993) measured wind profiles in nests of three species of birds in shortgrass prairie and found that the orientation of nests relative to vegetative cover did not correspond to the degree to which they were protected from prevailing winds. Nests of Lark Buntings (*Calamospiza melanocorys*) were placed on the leeward side of shrubs but experienced higher relative wind velocities (in the nest cup, compared with ambient conditions) than did the more exposed nests of Horned Larks and McCown's Longspurs (*Calcarius mccownii*). These results, in conjunction with the similarity in nest orientation displayed by different species in such a wide variety of ecosystems, suggest that protecting nests from solar radiation may be more important to open-nesting species than protecting nests from wind.

Several researchers have suggested that by placing nests on the northeast side of vegetation, birds maximize exposure to morning sun and minimize exposure to afternoon sun (Walsberg and King 1978, Verbeek 1981, Walsberg 1981, Petersen and Best 1991). At Becher's Prairie during the breeding season, the sun rises in the northeast and sets in the northwest. Nests with vegetation on the southwest side are thus exposed to sun in the morning but are shaded during the hottest time of the day. Our temperature data obtained from nests with different orientations showed that nests with vegetation on the southwest side heated up rapidly in the morning but remained cooler in the afternoon than did nests with vegetation on the northeast, southeast, or northwest sides. Wiebe and Martin (1997) documented a similar pattern of heating and cooling in White-tailed Ptarmigan (*Lagopus leucurus*) nests exposed to morning sun but shaded from afternoon sun. We believe that these microclimatic conditions provide the most thermally advantageous environment for eggs, nestlings, and attending adult birds.

Exposure of the nest to direct sun may result in dramatic changes in nest attentiveness during incubation (Zerba and Morton 1983b). Female Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) remained on nests exposed to direct sun to prevent embryos from reaching lethal temperatures (Zerba and Morton 1983a, b). A female with consecutive nests in the same breeding season had lower attentiveness during midday, and took longer and more frequent foraging bouts, at the nest that was more shaded than at the nest that was exposed to direct sun (Zerba and Morton 1983b). The lower afternoon temperatures that we recorded at Becher's Prairie in nests with vegetation on the southwest side should allow incubating adults to take more and longer foraging bouts during this time period than if vegetation were located on the northeast, southeast, or northwest side of the nest. In exposed nests, White-tailed Ptarmigan avoided taking incubation recesses during midday, when nest temperatures could rise above 45 C (Wiebe and Martin 1997). Lower afternoon temperatures should also be important during the nestling period, when foraging demands on attending adults are high. If nestlings are exposed to direct sun, adults must forego foraging opportunities to provide shade for nestlings, and they must expend energy to cool themselves and their young.

We found that nests with vegetation on the south and southwest sides but not on the east side had an additional advantage in that they heated up more quickly during the early morning than did other nests. If nests are exposed to direct sun during this period, eggs should cool less rapidly when adults leave the nest than if they were shaded. In fact, egg temperatures increase at rates directly related to ambient temperatures when eggs are exposed to direct sun (Zerba and Morton 1983a). Females may be able to take advantage of solar heating of eggs by increasing the length of their foraging bouts. Long foraging bouts and extended periods of nest attentiveness appear to be the most energy-efficient strategies for adults tending nests alone (Vleck 1981).

The most thermally favorable nest sites at Becher's Prairie appear to be those with several clumps of vegetation arranged around the southeast to west sides of the nest. These nests, however, accounted for only 5% of the 122 nests we found. The high percentage of nests (77%) we found beside a single clump of vegetation could indicate that sites with multiple clumps are limited in availability, or that they are less preferred because predation risk is higher. Nests with multiple clumps may also be under-represented in our sample because they were more difficult to find.

Differences in nest orientation may or may not result in differences in reproductive success. Nests of Verdins (*Auriparus flaviceps*) and Cactus Wrens (*Campylorhynchus brunneicapillus*) that were oriented into prevailing winds had higher success rates than did nests that were "incorrectly" oriented (Austin 1974, 1976). Verbeek (1981) compared success of Water Pipit (*Anthus spinoletta*) nests with different orientations and found no significant difference between nests oriented in the mean direction and other nests. If adults are able to adjust their nest-attendance behavior to provide protection for eggs and young, then effects of nest orientation may not be reflected in differences in embryo viability and nestling survival. Differences in nest orientation are more likely to be reflected in differences in nestling growth rates and post-fledging survival, and/or in sublethal behavioral costs to attending adults. Adults that expend less energy shading eggs and young from extreme heat and are able to take more and longer foraging recesses may be in better condition when young fledge and at the end of the breeding season. These factors may in turn influence renesting ability and adult survival probabilities, respectively. We plan to monitor Horned Lark and Vesper Sparrow nests through the incubation and nestling periods to determine how nest orientation influences nest-attendance behavior and renesting ability. Experiments involving manipulation of vegetative cover around nests would also provide valuable information on the importance of nesting cover to reproductive success and survival.

We found that other important determinants of nest temperature were the height and amount of cover provided by sheltering vegetation. A nest located beside a small clump of vegetation with little overhead cover was afforded scant protection from direct sun, even though the vegetation was located on the southwest side of the nest. Practices, such as prescribed burning, that remove standing litter from previous years' growth effectively eliminate large clumps of bunchgrass. We plan to investigate the impact of grassland fires on the availability of thermally advantageous nest sites for Horned Larks and Vesper Sparrows.

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