

RACIAL DIFFERENCES IN NESTS OF WHITE-CROWNED SPARROWS

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ABSTRACT.—I compared the nests of Eastern White-crowned Sparrows (*Zonotrichia leucophrys leucophrys*) from a subarctic area in Manitoba, Canada, Mountain White-crowned Sparrows (*Z. l. oriantha*) from subalpine meadows in California and Colorado, and Nuttall's White-crowned Sparrows (*Z. l. nuttalli*) from the coast of California. The nests were open bowls lined with fine grasses. They had a more or less bulky frame of twigs, the woody stems of shrubs, leaves, bark, and/or coarse grasses. Small amounts of many other items were buried in them.

The adults of these races are about the same size, but their nests are not. Nests of *Z. l. oriantha* were the largest, those of *Z. l. leucophrys* the smallest, and those of *Z. l. nuttalli* intermediate in size. Mountain White-crowned Sparrows build on and above the ground: their elevated nests were much larger than their ground nests. All nests blocked out 96–99% of air currents to which they were exposed. This characteristic is particularly well-suited to the windy conditions that prevail on the breeding grounds.

The nest's overall thermal conductance was significantly higher in *Z. l. leucophrys* than in the other races, even though *Z. l. leucophrys* nest under colder and wetter ambient conditions than the other two. They build their nests *in* the ground, however, which probably provides additional insulation and certainly reduces exposure to drafts. Thermal conductance was significantly related to the nest's mass and several of its dimensions, but was not simply a function of nest size. For example, the thermal conductance of the nest wall depended on the wall's porosity, but not on its thickness. Thermal conductance is not only a quantitative measure of the nest's insulation, but also it can be used to estimate the energetic cost of incubation.

The races of White-crowned Sparrows (*Zonotrichia leucophrys*) include a non-migratory form (*Z. l. nuttalli*) from the coast of California (Mewaldt et al. 1968, Mewaldt and King 1977), a short-distance migrant (*Z. l. oriantha*) which winters at low elevations in the southwestern United States and summers at high elevations in the Sierra Nevada Mountain Range (Morton et al. 1972, Walsberg and King 1978), and a middle-distance migrant (*Z. l. leucophrys*) which winters in the eastern United States and spends the summer in Canada (Austin 1968, Rees 1973). The breeding areas of these races are geographically separate and climatically quite different from one another. *Z. l. nuttalli* experience mild conditions at their breeding stations in the coastal fog zone of California. For example, at Lompoc, California, extreme temperatures during the breeding season (April–May) are 7 and 20°C, 21–23 days a month are either sunny or at most partly cloudy, precipitation is a scant 6–33 mm, and prevailing winds average only 3.6–3.7 ms⁻¹ (Ruffner 1978). In contrast, *Z. l. oriantha* nesting at Tioga Pass, California, experience ambient temperatures near freezing at night, extreme temperatures that range between -8 and 25°C, early morning winds that are both cold

and “brisk,” and frequent storms (Zerba and Morton 1983). Populations of *Z. l. leucophrys* nesting at Churchill, Manitoba, Canada, experience even harsher climatic conditions. For example, in 1978, extreme temperatures were 0 and 15°C, precipitation (both rain and snow) 26–81 mm, winds 9–25 ms⁻¹, and hours of sunshine only 8–9 per day.

These races differ phenotypically and physiologically (e.g., in their photoperiodic responses; Lofts and Murton 1968, Mewaldt et al. 1968, Murton and Westwood 1977) in ways that are adaptive and likely increase their breeding success in the nesting areas. Does genetic plasticity also exist in their nest-building behavior and therefore in the structure of their nests? Are they able to change the structure of the nest to fit the prevailing conditions to which they are exposed while nesting and to increase their breeding success in this way? Or, is nest structure (and the genetic program responsible for it) fixed and immutable, irrespective of climatological differences in the breeding areas? If the latter is the case, then breeding success may depend more on factors such as the nest's location and the parents' attendance to clutch and chicks than on the nest itself. Furthermore, since the nest is distorted by nestling

Zonotrichia as they mature, does its insulating capacity change during the brooding period? These questions were the focus of my study.

MATERIALS AND METHODS

COLLECTION SITES

Z. l. nuttalli. Nests of Nuttall's White-crowned Sparrows were collected at Vandenburg Air Base (34°N, 120°W, 95 m elev.) 16 km NW of Lompoc, Santa Barbara County, California, during April and May 1980–1981. This area is part of the coastal sage community, the dominant plants of which include sagebrush (*Artemisia californica*), sage (*Salvia* spp.), *Baccharis* spp., and *Happlopappus* spp. (Mooney 1977; E. Zerba, unpubl.).

Z. l. oriantha. Nests of Mountain White-crowned Sparrows came from Tioga Pass, Mono County, California (38°N, 107°W), and Gothic and Cumberland Pass, Gunnison County, Colorado (39°N, 107°W). They were collected in subalpine meadows (2,865–3,658 m elev.) during June and July 1978–1980. Dominant plants in these openings include willows (*Salix* spp.), grasses, sedges, and flowering annuals. Along the edges of these meadows are small stands of jeffrey and lodgepole pine (*Pinus jeffreyi* and *P. contorta*; California only), Engelmann spruce (*Picea engelmannii*; Colorado only), and quaking aspen (*Populus tremuloides*; California and Colorado; Rundel and Parsons 1977; Zerba and Morton 1983; C. Carey, unpubl.).

Z. l. leucophrys. Nests of Eastern White-crowned Sparrows were collected during June and July 1978 at Churchill, Manitoba, Canada (58°N, 93°E), which lies on the west side of Hudson Bay. The area is flat and low in elevation (35 m) and at the ecotone between northern arctic tundra and subarctic high boreal forest (taiga). Its ridges are sprinkled with glacier-smoothed boulders, open stands of black spruce (*Picea mariana*), and lichens; hollows are filled with bog and muskeg vegetation; and extensive areas of peat grow there. The ground cover is dominated by mosses (e.g., *Sphagnum*), lichens, low vascular plants, and scattered tall shrubs (e.g., willows; Ritchie 1959).

Nests from each of these areas were labeled, wrapped in heavy aluminum foil, and forwarded to me, together with descriptions of the nest site and the stage of the sparrow's breeding cycle when its nest was taken.

LABORATORY STUDIES OF THE NESTS

Nest's dimensions and the area of the nest cup. I weighed each nest and measured the following dimensions: (1) height, (2) thickness of the walls at mid-height (an average value based on measurements at eight locations spaced equal-

ly around the nest's circumference), (3) thickness of the floor, (4) major and minor diameters of the nest and the nest cavity, and (5) depth of the nest cavity. I also calculated the cross-sectional area of the nest and nest cavity. I assumed that both were elliptical in shape, in which case the cross-sectional area is $(\pi/4)ab$, a and b being the major and minor diameters of the nest or nest cup.

Finally, I determined the surface area of the nest cavity by using a piece of thin rubber sheet cut to fit it and following the method of Kern and van Riper (1984).

Physical properties of the nests. I measured the *thermal conductance* (h) of the nest's floor (h_f) and thinnest wall (h_w) and used this information to estimate what I call the "overall thermal conductance" (h_{wt}) of the nest. The *porosity* of the nests was measured with the aid of light in two ways: use of a photometer and with photographic enlarging paper. Because the three races of White-crowned Sparrows involved in this study typically nest in areas that are windy, I also determined their *wind resistance*. To do so, I measured airflow on the internal and external surfaces of nests exposed to laminar airstreams. All of these properties were determined following the methods of Kern and van Riper (1984).

Nest composition. At the end of the study, I dismantled many nests of *Z. l. nuttalli* and *oriantha* and weighed the materials of which they were made. I did not, however, disassemble the nests of *Z. l. leucophrys* because I had only seven of them. Where possible, I identified the plants in the nests using information about the local vegetation at each collection site from Jepson (1923), Ritchie (1959), and Barbour and Major (1977). Some of my identifications are necessarily tentative because the nests contained few flowering parts.

Statistical analyses. I evaluated the data with one-way analysis of variance followed by Student-Newman-Keuls (multiple range) tests, Student's t -tests, or least squares analyses, depending on the data set (Zar 1974). Percentages were converted to their arcsin equivalents before analysis. The values that appear in the text and tables of this paper are means \pm 95% confidence intervals. Only nests of average or better-than-average quality were used in the analyses.

RESULTS

LOCATION OF NESTS

Z. l. nuttalli. Nearly all of the nests were in *Baccharis* or sagebrush. Rarely, they were located in *Happlopappus* or mustard (Cruciferae). Nest height above the ground averaged 41.1 ± 4.4 cm ($n = 54$).

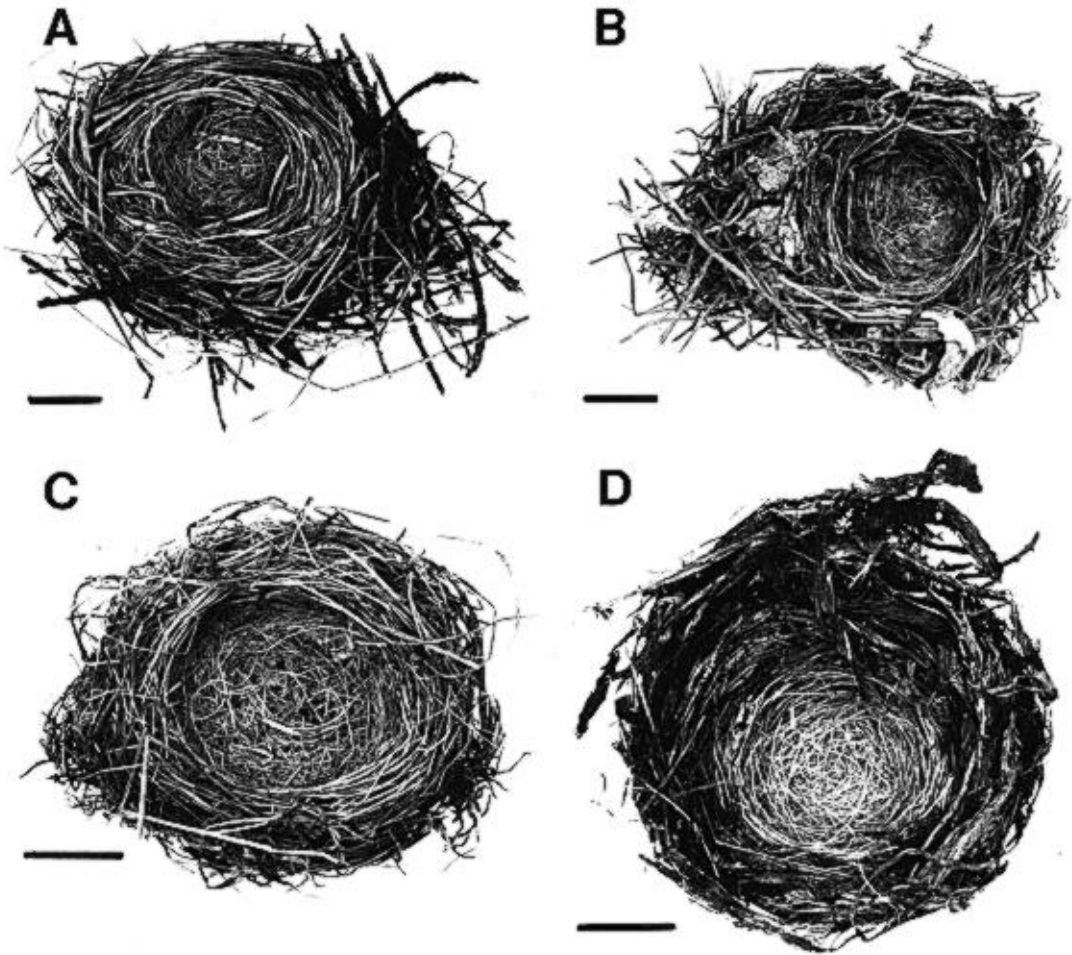


FIGURE 1. Nests of White-crowned Sparrows: A, Montane race (*Z. l. oriantha*); B, Coastal race (*Z. l. nuttalli*); C, Eastern race (*Z. l. leucophrys*)—type found in vegetation in the ground; D, Eastern race—type found wedged into gravel banks and reinforced with strips of bark. The lines represent a length of 3 cm.

Z. l. oriantha. Elevated nests at Tioga Pass were in willows (11 of 17 nests) and lodgepole pines. At Gothic and Cumberland Pass, they were in willows (six of eight nests) and Englemann spruce. Nest height above the ground averaged 69.4 ± 22.1 cm ($n = 17$) and was significantly higher than that of nests of *Z. l. nuttalli* ($P < 0.001$, t -test). Nests that were built on the ground were at the base of willows or in clumps of grass.

Z. l. leucophrys. Nests were in the ground at the bases of purple willow (*S. planifolia*), dwarf birch (*Betula glandulosa*), black spruce, white spruce (*P. glauca*), buckberry (*Shepherdia canadensis*), and poplars (*Populus balsamifera*). These trees were 30–76 cm high.

NEST COMPOSITION AND SIZE

Nests of the three races were similar in construction, although they differed considerably in size and external appearance (Fig. 1) and were made of somewhat different materials

(Tables 1 and 2). All were open bowls lined with fine grasses and supported by an outer frame, the size and nature of which depended on the nest's location.

Z. l. nuttalli. The bulky outer frame of the nest (60–95% of its mass) contained substantial amounts of grass (of all sizes), white-woolly stems bearing flowers in terminal clusters (a composite, perhaps *Eriophyllum* spp.), and leaves. Sagebrush leaves were abundant (6–58% of the frame's mass) in all seven nests that were built in *Artemisia*. *Baccharis* leaves occurred in four of nine nests that were built in *Baccharis* (forming 12–65% of the frame's mass), but in only one of the nests built in *Artemisia* (accounting for only 1.2% of the nest's mass). Tiny ovate leaves, possibly from *Eriogonum*, were also common in the frame. Minor items such as fecal pellets, thread, seed pods (Cruciferae), burrs, and empty pupal cases of flies, were also buried in the frame (Table 2). Pupal cases were not as numerous as in the

TABLE 1. Composition of nests of Mountain and Nuttall's White-crowned sparrows. Values in the table are means (range) [number of nests containing this item]. Data are for the entire nest.

	<i>Z. l. oriantha</i>		<i>Z. l. nuttalli</i>	
	Elevated nests	Ground nests	Nests in <i>Baccharis</i>	Nests in <i>Artemesia</i>
<i>n</i>	17	5	9	7
Mass (in g)	38.9 (22.6–74.5)	18.2 (9.7–37.9)	29.7 (17.1–45.0)	39.4 (24.7–53.9)
Blades and culms of grass (% total mass) ^a				
Very fine	—	—	6.2 (0–18.3) [5]	7.9 (0–20.0) [6]
Fine	15.7 (0–32.0) [16]	18.9 (0–35.5) [4]	8.6 (0–19.1) [6]	4.1 (0–15.2) [6]
Medium	23.1 (0–55.1) [16]	50.9 (25.3–74.7) [5]	9.0 (0–26.9) [6]	8.8 (0–35.5) [3]
Coarse	25.3 (0–68.2) [16]	8.4 (0–19.5) [3]	8.0 (0–41.0) [4]	20.1 (0–44.6) [5]
Stems of woody shrubs and herbs (% total mass) ^a				
Fine	—	—	0.3 (0–2.8) [1]	2.0 (0–7.6) [3]
Medium	—	—	8.4 (0–24.5) [6]	1.6 (0–4.9) [4]
Coarse	—	—	3.2 (0–11.6) [3]	14.9 (0–80.3) [4]
Woolly stems and flower heads of Compositae (% total mass)				
	—	—	17.3 (0–68.5) [6]	5.6 (0–26.6) [4]
Twigs (% total mass)				
	16.1 (0.7–74.5) [17]	4.8 (0.6–14.8) [5]	—	—
Evergreen twigs (no./nest)	11.3 (0–96)	0.6 (0–2)	—	—
Deciduous twigs (no./nest)	48.0 (3–139)	21.6 (0–74)	—	—
Strips and bits of bark (% total mass)				
	2.8 (0–17.6) [10]	1.5 (0–7.7) [1]	—	—
Leaves (% total mass)				
<i>Baccharis</i> spp.	—	—	18.3 (0–65.1) [4]	0.2 (0–1.2) [1]
<i>Artemesia</i> spp.	—	—	16.2 (0–55.3) [5]	29.3 (5.7–57.9) [7]
<i>Erigonum</i> spp.?	—	—	4.2 (0–29.4) [4]	0.1 (0–0.4) [3]
Other ^b	7.1 (0–30.1) [16]	1.9 (0–8.4) [4]	—	2.4 (0–14.4) [3]
Duff ^c	5.5 (0–17.2) [11]	10.4 (0–19.0) [3]	—	0.3 (0–1.3) [3]

^a Very fine, fine, medium, and coarse denote relative size.

^b For *Z. l. oriantha*, most of the leaves were from willows (*Salix* spp.).

^c Bits of grass, leaves, twigs, and/or soil.

nests of *Z. l. oriantha* (below), but they occurred in three of nine nests built in *Baccharis* and two of seven built in sagebrush.

The nest lining consisted of grasses (medium to very fine), the stems of shrubs, many *Artemesia* leaves, some "duff" (=bits of grass, leaves, twigs, and soil), and a few white-woolly plant stems, flower heads (Compositae), rhizomes, feathers, hair or tufts of rodent fur, and bits of waxed paper. By mass, the liner constituted 25.8% (range: 11–40%, *n* = 5) of nests built in sagebrush; and 15.3% (range: 4–26%, *n* = 9) of nests built in *Baccharis*.

Z. l. oriantha. The outer frame accounted

for more than 80% of the nest's mass and contained twigs, leaves, bark, and the blades and culms of large grasses (Table 1). Duff, fecal pellets (rabbit, bird), parts of insects, small sedges, mosses, and herbs, and tiny dirt balls were buried within it (Table 2). The coarse grasses were probably wheat grass (*Agropyron* spp.), western rye grass (*Elymus glaucus*), and/or California brome grass (*Bromus carinatus*), all of which are common in woodland meadows above 1800 m elevation in the Sierra Nevada Mountains (Rundel and Parsons 1977). Some of the bark was from evergreens, and some from quaking aspen. Most of the leaves

TABLE 2. Minor items frequently present in the nests of Mountain and Nuttall's White-crowned sparrows. Values in the table are numbers of nests that contained each item.

Item	<i>Z. l. oriantha</i>		<i>Z. l. nuttalli</i>		Comments
	Elevated nests	Ground nests	Nests in <i>Baccharis</i>	Nests in <i>Artemisia</i>	
Number of nests examined	17	5	9	7	
Animal products					
Feathers	8	1	2	1	Usually small
Hair	13	2	3	2	Commonly numerous
Porcupine quills	5	2	0	0	
Fecal pellets	2	0	1	1	Rabbit or bird
Human products					
Thread or fishing line	3	0	1	0	
Bits of plastic or waxed paper	1	0	0	1	
Invertebrates					
Gastropod (snail) shell	1	0	0	0	
Lady beetles, flies, caterpillars, exoskeletons, pupal cases, chrysalises	7	1	4	2	Most commonly empty pupal cases of flies
Plants and plant parts					
Seed pods and catkins	3	1	1	0	Catkins of <i>Salix</i> spp., seed pods of Cruciferae
Lichens	1	0	0	0	
Moss	3	2	0	0	
Fine sedges	4	1	0	0	
Small herbs	1	0	1	1	Whole plants
Roots, rootlets, rhizomes	5	0	0	2	
Pine needles	7	0	0	0	
Burrs	0	0	2	0	
Dirt balls	5	1	0	0	Always tiny

were from willows. In many cases, they had the character of leaf-mold. Some of the twigs exceeded 15 cm in length and formed a conspicuous platform under the rest of the nest (Fig. 1A), but most of them were smaller and buried within it. They ranged in number from 3 to 198 per nest. All of the elevated nests that I examined, whether built in willows (11 nests) or evergreens (six nests), contained deciduous twigs, as did four of five ground nests. However, only seven elevated and two ground nests contained evergreen twigs. On average, there were 11 evergreen and 48 deciduous twigs in elevated nests, but only <1 evergreen and 22 deciduous twigs in ground nests. Several elevated (only) nests (Table 1) also contained pine and fir (*Abies* spp.) needles. The most common insect parts were empty pupal cases of flies: I counted 48 in one nest.

The linings of these nests (15.7 and 18.9% of the mass of elevated [$n = 17$] and ground [$n = 5$] nests, respectively) consisted mainly of fine grasses, plus a few tiny feathers, porcupine quills, bits of plastic, thread, and/or shredded fishing line (Table 2).

Z. l. leucophrys. The outer frame contained strips of bark (three nests), fine grasses (six), leaves and twigs (one), moss (one), and a large feather (one). The liner contained fine grasses (seven), small feathers (five), and hair (two).

The nests of the three races differed in mass,

cross-sectional area, and height (Table 3), even though the adult sparrows are about the same size. The nests of *Z. l. oriantha* were the largest (Fig. 1A), those of *Z. l. leucophrys* the smallest (Fig. 1C, D), and those of *Z. l. nuttalli* intermediate in size (Fig. 1B). Nests of *Z. l. nuttalli* and *oriantha*, which were built on or above ground, generally had much thicker walls and floors than those of *Z. l. leucophrys*, which were built in the ground (Table 3). In all three races, the nest cups were similar ($P > 0.05$) in depth and cross-sectional area. However, there was significantly less surface in the nest cup of *Z. l. nuttalli* than in nests of the other two races. This probably indicates that the shape of the nest cup differs among the races.

My limited data suggest that the elevated nests of *Z. l. oriantha* are larger than their ground nests: those in my sample were significantly heavier, taller, and had a thicker floor than ground nests (Table 3).

RACIAL DIFFERENCES IN THE NEST'S INSULATION

Of these races of White-crowned Sparrows, *Z. l. leucophrys* had the smallest, thinnest, most porous (highest % P_{light}), and least insulating (the highest h and % P_{air}) nests (Table 3). *Z. l. oriantha* and *nuttalli* built elevated nests that were larger and thicker than those of *Z. l. leu-*

TABLE 3. Racial differences in the nests of White-crowned Sparrows. The nests used for this summary were collected from females during egg-laying or incubation. Sample sizes that differ from those in the "n" row are presented in parentheses within the table.^a

Characteristic	<i>Z. l. leucophrys</i>			<i>Z. l. nuttalli</i>			<i>Z. l. orientalis</i>			
	n	7	31	12	4	n	7	31	12	4
Nest's mass (g)		20.9 ± 11.0	32.1 ± 4.3	48.6 ± 9.9						25.0 ± 22.0
Nest's dimensions (cm)										
Walls		2.6 ± 0.9	3.4 ± 0.3	3.8 ± 0.5						3.8 ± 1.9
Thinnest wall		1.3 ± 0.4	2.0 ± 0.2	2.3 ± 0.5						2.2 ± 0.6
Floor		2.1 ± 0.3	3.8 ± 0.5	3.9 ± 1.0						2.1 ± 1.0
Height		5.6 ± 0.6	7.9 ± 0.4	8.7 ± 1.0						5.9 ± 2.5
Depth of nest cavity		3.5 ± 0.5	3.7 ± 0.2	3.8 ± 0.6						3.8 ± 1.6
Surface area of nest cavity (cm ²)		73.5 ± 9.5	58.9 ± 11.4	71.5 ± 7.3						70.3 ± 26.1
Cross-sectional areas (cm ²)										
Nest cavity		29.1 ± 2.3	27.7 ± 1.6	29.3 ± 2.0						28.6 ± 6.0
Nest		113.7 ± 35.1	152.4 ± 14.3	238.7 ± 25.8						182.6 ± 113.6
Wind resistance (% P_{air}) ^b										
Walls		3.54 ± 0.35	1.55 ± 0.02 (29)	1.07 ± 0.05 (11)						3.83 (3)
Floor		3.00 ± 0.51	0.68 ± 0.01 (29)	0.63 ± 0.06 (9)						1.82 (2)
Nest's porosity—penetration by light (% ^c)										
% P_{light} —walls ($\times 10^{-2}$)		20.74 ± 8.10	4.09 ± 0.40 (24)	6.70 ± 2.82 (9)						6.10 (3)
—floor ($\times 10^{-2}$)		1.94 ± 1.30	0.19 ± 0.01 (24)	1.48 ± 0.27 (9)						0.66 (2)
% $A_{exposed}$ —walls		24.33 ± 6.76 (6)	11.29 ± 0.91 (30)	7.36 ± 1.86 (11)						16.37 ± 5.31
Thermal conductance (W m ⁻² °C ⁻¹)										
Walls (h_w)		9.43 ± 2.89	7.01 ± 0.51 (32)	6.81 ± 1.78 (11)						8.08 ± 2.45
Floor (h_f)		3.46 ± 0.44	2.96 ± 0.14 (32)	2.99 ± 0.29						4.07 ± 1.05
Overall (h_{wt})		6.44 ± 1.35	4.98 ± 0.27 (32)	4.89 ± 0.91 (11)						6.07 ± 1.18
Weight-specific thermal conductance (W m ⁻² °C ⁻¹ g ⁻¹)		0.40 ± 0.20	0.18 ± 0.03 (32)	0.11 ± 0.03 (11)						0.30 ± 0.26

^a For *Z. l. leucophrys*, *Z. l. nuttalli*, and the elevated nests of *Z. l. orientalis*, underlined values in each row are not significantly different from one another; values that are not underlined differ significantly from the other values in the row ($P < 0.05$; Student-Newman-Keuls test). Ground nests of *Z. l. orientalis* were not included in the interracial analyses because of their small number. They were, however, compared with elevated nests of the same race; significant differences (determined with Student's t -tests) are indicated by the P values between pairs of means in the last two columns of the table.

^b % P_{air} = amount of an incident airstream that penetrates a nest, expressed as a percent; % P_{light} —walls = amount of incident light that penetrates the walls of the nest, expressed as a percent; % P_{light} —floor = amount of incident light that penetrates the floor of the nest, expressed as a percent; % $A_{exposed}$ —walls = area of photographic paper lining the walls of the nest cup that is exposed when the outside of the nest is subjected to a 1-s pulse of light. For more complete definitions of these terms, see Kern and van Riper (1984).

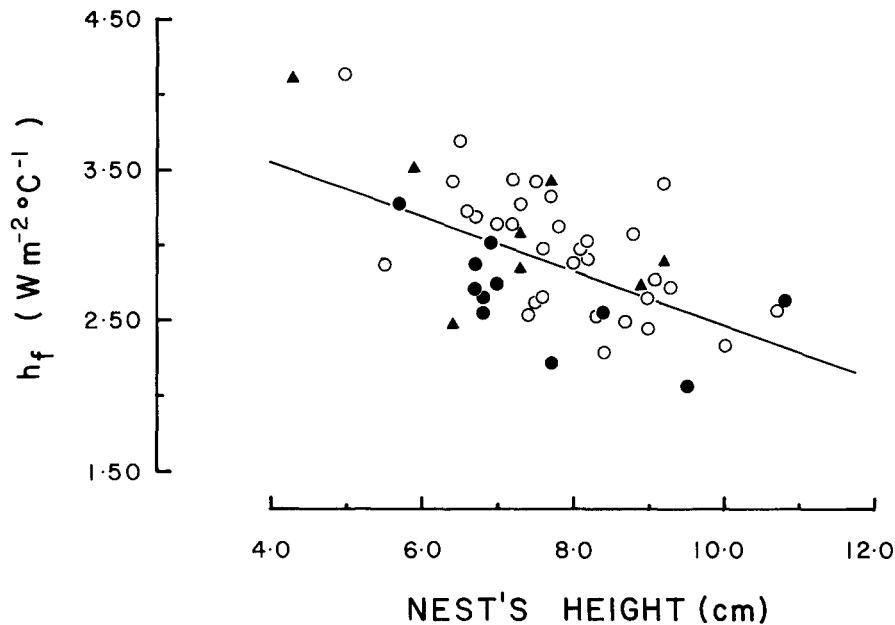


FIGURE 2. In the coastal race of White-crowned Sparrows (*Z. l. nuttalli*), the nest's h_f and intrinsic height are significantly related ($r = -0.5691$, $P < 0.001$, 52 df). Symbols represent nests collected from egg-laying and incubating (O) and brooding (▲) females, or postfledging (●). The equation for the best-fit line that is shown in the figure is $h_f = 4.35 - 0.19H$, in which H is the nest's height.

cophrys, significantly less porous, and that leaked heat less readily, i.e., had significantly smaller h_{wf} , especially on a weight-specific basis (Table 3). They also blocked out 98–99% or more of wind-streams to which they were exposed.

The thermal conductance of the nest was significantly related to several of its dimensions and to its mass, both in *Z. l. oriantha* and *nuttalli* (Table 4, Fig. 2). A particularly

high positive correlation existed between h_w and % P_{light} through the walls of the nest; and particularly high negative correlations existed between h_f and the thickness of the nest's floor and the nest's height.

The thermal conductance (h_w and h_{wf}) of elevated nests of *Z. l. oriantha* was significantly correlated with the height of the nest above the ground ($r = 0.4970$ and 0.5429 , respectively; 21 df; $P < 0.02$ and < 0.01 , respective-

TABLE 4. Significant correlations between thermal conductance (h) and other characteristics of the nests of Mountain and Nuttall's White-crowned sparrows. Values in the table are correlation coefficients (r).

Race	n	Characteristic of the nest	Thermal conductance ^a		
			h_w	h_f	h_{wf}
<i>Z. l. oriantha</i> ^b	29	Nest's mass	—	-0.5051*	—
		Thickness of the nest's floor	—	-0.5894**	-0.4743*
		Nest's height	—	-0.5547**	—
		Surface area of the nest cavity	—	-0.4619*	—
		Cross-sectional area of the nest	—	-0.5203*	—
		% P_{light} —walls ^c	0.6885*	—	—
<i>Z. l. nuttalli</i>	54–55	Nest's mass	—	-0.4559***	-0.3094*
		Thickness of the nest's floor	—	-0.4398**	-0.2960*
		Nest's thinnest wall	-0.3050*	—	-0.3139*
		Nest's height	—	-0.5691***	—
		Surface area of the nest cavity	0.3104*	—	—
		Cross-sectional area of the nest	—	-0.2809*	—
		Cross-sectional area of the nest cavity	0.3763**	—	-0.3117*
		% A_{exposed} —walls ^c	0.3989*	—	—
		% P_{light} —walls ^c	0.6610***	—	—
<i>Z. l. leucophrys</i>	7	Thickness of the nest's floor	—	-0.9050**	—

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

^b Data are for elevated and ground nests combined.

^c See Table 3 for definitions of these terms.

TABLE 5. Variations in the elevated nests of Mountain and Nuttall's White-crowned sparrows according to the stage of the breeding cycle. Sample sizes that differ from those in the "n" row are presented in parentheses within the table. Significant differences between stages exist only in the surface area and cross-sectional area of the nest cavity and in the wind resistance of the nest's floor (see footnote).

Characteristic	<i>Z. l. orientalis</i>			<i>Z. l. nuttalli</i>		
	Egg-laying and incubating	Postfledging	Egg-laying and incubating	Brooding	Postfledging	Postfledging
<i>n</i>	12	5	31	8	12	12
Nest's mass (g)	48.6 ± 9.9	40.8 ± 22.4	32.1 ± 4.3	30.9 ± 9.5	35.8 ± 9.5	35.8 ± 9.5
Nest's dimensions (cm)						
Walls	3.8 ± 0.5	3.7 ± 0.8	3.4 ± 0.3	3.4 ± 0.4	3.4 ± 0.3	3.4 ± 0.3
Thinnest wall	2.3 ± 0.5	1.8 ± 0.1	2.0 ± 0.2	1.8 ± 0.6	2.0 ± 0.4	2.0 ± 0.4
Floor	3.9 ± 1.0	3.8 ± 1.7	3.8 ± 0.5	3.3 ± 0.9	3.8 ± 1.1	3.8 ± 1.1
Height	8.7 ± 1.0	7.2 ± 1.3	7.9 ± 0.4	7.1 ± 1.3	7.5 ± 0.9	7.5 ± 0.9
Depth of nest cavity	3.8 ± 0.6	3.0 ± 0.7	3.7 ± 0.2	3.7 ± 0.6	3.2 ± 0.4	3.2 ± 0.4
Surface area of nest cavity (cm ²) ^a	71.5 ± 7.3	72.0 ± 8.9	58.9 ± 11.4	68.8 ± 11.9	67.2 ± 4.3	67.2 ± 4.3
Cross-sectional areas (cm ²)						
Nest cavity ^a	29.3 ± 2.0	37.9 ± 7.8	27.7 ± 1.6	31.0 ± 4.4	35.2 ± 3.0	35.2 ± 3.0
Nest	238.7 ± 25.8	258.8 ± 99.1	152.4 ± 14.3	147.7 ± 22.4	166.7 ± 10.8	166.7 ± 10.8
Wind resistance (% P_{air}) ^b						
Walls	1.07 ± 0.05 (11)	1.36 (2)	1.55 ± 0.02 (29)	1.30 ± 0.11	1.00 ± 0.08 (7)	1.00 ± 0.08 (7)
Floor ^a	0.63 ± 0.06 (9)	2.10 (2)	0.68 ± 0.01 (29)	1.02 ± 0.17	0.36 ± 0.01 (7)	0.36 ± 0.01 (7)
Nest's porosity—penetration by light (%) ^b						
% P_{light} —walls ($\times 10^{-2}$)	6.70 ± 2.82 (9)	2.67 (3)	4.09 ± 0.40 (24)	5.01 ± 1.48 (7)	11.28 ± 3.06 (9)	11.28 ± 3.06 (9)
—floor ($\times 10^{-2}$)	1.48 ± 0.27 (9)	1.49 (3)	0.19 ± 0.01 (24)	0.16 ± 0.16 (7)	0.13 ± 0.02 (9)	0.13 ± 0.02 (9)
% $A_{exposed}$ —walls	7.36 ± 1.86 (11)	...	11.29 ± 0.91 (30)	2.99 ± 0.57	12.60 ± 4.38 (10)	12.60 ± 4.38 (10)
Thermal conductance (W m ⁻² °C ⁻¹)						
Walls (h_w)	6.81 ± 1.78 (11)	6.97 ± 1.97	7.01 ± 0.51 (32)	7.58 ± 1.63	7.79 ± 2.00	7.79 ± 2.00
Floor (h_f)	2.99 ± 0.29	3.14 ± 0.97	2.96 ± 0.14 (32)	3.12 ± 0.45	2.56 ± 0.29	2.56 ± 0.29
Overall (h_{wo})	4.89 ± 0.91 (11)	5.05 ± 1.36	4.98 ± 0.27 (32)	5.35 ± 0.76	5.18 ± 1.08	5.18 ± 1.08
Weight-specific thermal conductance (W m ⁻³ °C ⁻¹ g ⁻¹)						
h_{wo}/g	0.11 ± 0.03 (11)	0.15 ± 0.11	0.18 ± 0.03 (32)	0.20 ± 0.07	0.17 ± 0.07	0.17 ± 0.07

^a For each race, means are significantly different ($P < 0.05$) from one another if *not* joined by the same line; those so joined do not differ significantly ($P > 0.05$; Student-Newman-Keuls test).

^b See Table 3 for definitions of these terms.

ly); in other words, nests near the ground were better insulated than those that were more aloft. However, insulation and the distance of the nest from the ground were not correlated in *Z. l. nuttalli* ($r = 0.0331$ and 0.0026 for h_w and h_{wf} , respectively; 52 df).

In *Z. l. oriantha* and *nuttalli*, h_w appeared to be related to the porosity rather than the thickness of the walls. It was significantly correlated with % A_{exposed} in *Z. l. nuttalli* and with % P_{light} in both races (Table 4), but not significantly correlated with the average thickness of the nest's walls in either race ($r = -0.0138$ and -0.0709 for *Z. l. oriantha* and *nuttalli*, respectively; 27 and 53 df).

Since in *Z. l. oriantha* elevated nests had thicker floors than ground nests, but walls of similar thickness (Table 3), I was not surprised to find that elevated nests lost heat less rapidly than ground nests via their floor ($P < 0.005$), but at the same rate via their walls. The similarity in h_w of the two types of nests was, however, puzzling in view of my finding that the walls of ground nests permitted significantly more air ($P < 0.05$) to pass through them than did the walls of elevated nests (Table 3).

EFFECTS OF CHICKS ON NESTS OF *Z. l. nuttalli* AND *Z. l. oriantha*

Growing chicks distorted the nest cup as illustrated by changes in the cross-sectional area of the nest cavity in both *Z. l. oriantha* and *nuttalli* between the incubation and postfledging stages of the nesting cycle. Nestlings also increased the surface area of the nest cavity in *Z. l. nuttalli* between the incubation and brooding stages (Table 5). Other dimensions of the nest did not change appreciably. Enlargement of the nest cup did not, however, affect the nest's h , at least in elevated nests for which I had sufficient data for analysis (Table 5).

DISCUSSION

RELATIVE IMPORTANCE OF THE NEST AND ITS LOCATION

Zerba and Morton (1983) found that the mean temperature of the eggs (T_e) of *Z. l. oriantha* was significantly lower and less stable in elevated nests than in ground nests, probably because the former are subjected to more convective cooling than the latter. The elevated nests of this race, however, are larger, have thicker, less porous floors, and lose heat through the floor at a significantly slower rate than ground nests when studied under laboratory conditions (Table 3). In short, they are better insulated than ground nests. Perhaps the increased insulation offsets the increased convective cooling to which they are exposed. Al-

ternatively, ground nests may be less well insulated because (1) they are not subjected to as much convective cooling, or (2) the vegetation and soil around them provide additional insulation.

In like manner, the nests of *Z. l. leucophrys* are not maladapted to the harsh climatic conditions at Churchill, Manitoba, even though they are small, thin, and not highly insulated as compared with nests of the other two races (Table 3). These sparrows build their nests in mats of vegetation on the ground, and such vegetation (sphagnum and other mosses) probably adds to the overall insulation of the nest. In cases where nests of *Z. l. leucophrys* are wedged into cut banks and therefore partially exposed, the walls on the exposed sides are thicker than the other walls and reinforced with strips of bark (compare C and D in Fig. 1).

These differences in nests suggest that crowned sparrows tailor nest structure to the microclimate at the nest site. This is also suggested by the fact that in cool subalpine meadows there is an inverse relationship between the height of the nest above the ground and the nest's insulation (*Z. l. oriantha*; Table 4), but in the milder coastal breeding areas (*Z. l. nuttalli*) no such relationship exists. Furthermore, the elevated nests of *Z. l. oriantha* are significantly larger than those of *Z. l. nuttalli* (Table 3). Although the general design of the nest is probably genetically determined in *Zonotrichia*, it appears that adaptive variations are still possible.

Palmgren and Palmgren (1939) documented differences in the nests of several European songbirds relative to climatic variations between breeding areas. More recently, Schaefer (1980) reported differences in the nests of Northern Orioles (*Icterus galbula*) as a function of **latitude**, and Kern and van Riper (1984) described differences in the nests of Common Amakihi (*Hemignathus virens virens*) as a function of **elevation**. My data complement these and illustrate that **interracial** differences of an adaptive nature also occur in the nests of at least one passerine species.

Certainly the location of the nest is as important as nest composition and morphology in reducing the energetic cost of incubating a clutch of eggs. Many birds are believed to orient their nests so as to minimize thermal stress during incubation (Horvath 1964, Ricklefs and Hainsworth 1969, Balda and Bateman 1973, Calder 1973, Austin 1974, Conner 1975, Inouye 1976, Schaefer 1976, Högstedt 1978, Loman 1979, McEllin 1979, Shuster 1980, Inouye et al. 1981, Walsberg 1981; and many others cited in Rich [1980] and Zerba and Morton [1983]). In *Z. l. oriantha*, for example, nests

TABLE 6. Estimated energetic costs of incubation (H_p) in three races of White-crowned Sparrows (*Zonotrichia leucophrys*) at the extreme ambient temperatures to which incubating females would likely ever be exposed. These costs are based on the h_{wf} of the nest.

Race	Nesting conditions ^a			H_p required to keep T_e constant			
	Average T_{max} (°C)	Average T_{min} (°C)	Winds	(W)		(%MR) ^b	
				At T_{max}	At T_{min}	At T_{max}	At T_{min}
<i>Z. l. leucophrys</i>	15	0	Yes	0.129	0.184	31.9	45.4
<i>Z. l. nuttalli</i>	20	7	Yes	0.099	0.136	24.5	33.7
<i>Z. l. oriantha</i>	25	-8	Yes	—	—	—	—
Elevated nests	—	—	—	0.085	0.176	20.5	42.4
Ground nests	—	—	—	0.091	0.204	21.9	49.2

^a Sources of extreme maximal (T_{max}) and minimal (T_{min}) temperatures: *Z. l. leucophrys*—monthly climatological summaries for June and July 1978, weather station at Churchill, Manitoba, Canada; *Z. l. nuttalli*—climatological data for Santa Maria, California (Ruffner 1978), which is 43 km north of Lompoc, where the nests were collected; *Z. l. oriantha*—climatological data for Tioga Pass, California, during June–Aug. 1980 (Zerba and Morton 1983).

^b MR, is the metabolic rate during the inactive phase of the day and under basal conditions. It was determined with the equation of Aschoff and Pohl (1970) for passerines. For *Z. l. leucophrys* and *nuttalli*, MR, = 0.404 W; for *Z. l. oriantha*, 0.415 W.

are positioned in such a way that they (1) are exposed to the sun in the morning and shaded in the afternoon (Walsberg and King 1978), and (2) shielded from wind and storms (Zerba and Morton 1983). The same appears to be the case for nests of *Z. l. leucophrys* at Churchill, Manitoba. They are usually on the southern or southeastern sides of small trees, where they are shielded from cold winds coming from the north-northwest and west-northwest (Kern and deGraw, unpubl. obs.).

CHANGES IN THE NEST DURING THE BREEDING CYCLE

Nestling White-crowned Sparrows enlarge the nest cup and/or compress the material in the floor of the nest (i.e., reduce % P_{air}) as they mature (Table 5). Similar changes have been noted in the nests of other species including Blue Tits (*Parus caeruleus*; O'Connor 1975), Broad-tailed Hummingbirds (*Selasphorus platycercus*; Calder 1973), and Indigo Buntings (*Passerina cyanea*; Payne, unpubl. obs.). The changes in size of the nest cavity may develop simply because chicks grow in a confined space. However, such changes may also be adaptive in the sense that they allow more air flow around the chicks and prevent hyperthermia (O'Connor 1975). Nestling White-crowned Sparrows do apparently experience thermal

stress in the nest: they pant and appear restless in the nest when exposed to direct sunlight (Morton and Carey 1971). Like young Say's Phoebes (*Sayornis saya*; Weathers 1983), they sometimes leave the nest during the heat of the day and only return later when it is cooler.

USING NESTS TO ESTIMATE THE ENERGETIC COSTS OF INCUBATION

Kern and van Riper (1984) have suggested that the thermal conductance of the nest can be used, just as eggs have been used previously (Kendeigh 1973), to estimate the amount of energy required to keep the clutch warm during incubation. The size of h_{wf} indicates the rate at which heat leaves a nest per unit surface area of the nest cup and per unit difference in the temperature across the nest. Kern and van Riper proposed that the surface of the nest across which heat is lost from the clutch is roughly equivalent to the area of the parent's brood patch (A_{bp} ; 7.8 cm² for *Z. l. oriantha* [Walsberg and King 1978]); and that the temperature difference across the nest is about $(33.6 - T_a)$ °C, 33.6°C being the average nest temperature (T_n) reported for 11 species of passerines (Drent 1975) and T_a being ambient temperature. If T_e is to remain high and constant during incubation, the female parent must

TABLE 7. Energy required to keep eggs at temperatures compatible with embryonic development in selected passerine species.

Species	Energetic cost of incubation as a function of		Range of T_n 's for which incubation costs are applicable (°C)	Source
	MR of a bird in an empty nest	MR ^a		
House Wren (<i>Troglodytes aedon</i>)	—	22–10%	17–22	Kendeigh (1963)
Great Tit (<i>Parus major</i>)	52–39% higher	68–62%	0–16	Mertens (1977)
European Starling (<i>Sturnus vulgaris</i>)	27–23% higher	49–23%	(-10)–10	Biebach (1979)
Zebra Finch (<i>Poephila guttata</i>)	21–17% higher	37–21%	12–24	Vleck (1981)
Common Amakihi (<i>Hemignathus virens virens</i>)	—	47–19%	0–21	Kern and van Riper (1984)

^a % MR, = $\{[(MR \text{ of incubating bird in nest}) - (MR \text{ of bird in empty nest})] / MR_e\} \times 100$.

replace the heat lost from the clutch (\dot{H}_L) with an equal amount of metabolic heat (\dot{H}_P) as long as she remains in the nest each day (t_n , defined as the percent of each 24-h period during which the bird is in the nest; 72.7% for *Z. l. oriantha* [Morton and Carey 1971]). However, parents may leave the nest periodically, e.g., to forage. In their absence, the clutch cools and it must be rewarmed when they return. In a 24-h period, the energy required to rewarm the clutch is the product of the heat required to rewarm the eggs after each absence (\dot{H}_R) and the number of times the birds are away from the nest daily (t_r). Walsberg and King (1978) estimated that for *Z. l. oriantha*, $(\dot{H}_R)(t_r) = 0.061$ W. Accordingly, the energy necessary to keep the clutch at incubation temperature, i.e., the energetic cost of incubation (in W), is

$$\dot{H}_P = \dot{H}_L = (h_{wf})(A_{bp})(T_n - T_a)(t_n) + (\dot{H}_R)(t_r) \quad (1)$$

or in White-crowned Sparrows

$$\dot{H}_P = \dot{H}_L = (h_{wf})(7.8)(33.6 - T_a)(0.727) + 0.061 \quad (2)$$

By substituting values of h_{wf} from Table 3 and values of T_a that represent the most extreme to which incubating females would probably be exposed (Table 6) into equation 2, I estimate that the energetic cost of keeping the clutch warm is between 0.085 and 0.204 W or 21–49% of the basal metabolic rate of a White-crowned Sparrow during the rest (inactive) phase of the day (MR_r ; Table 6).

These costs of incubation are similar to those published for other passerines (Table 7) and to estimates of cost that can be calculated using Kendeigh's (1973) equation and data concerning the eggs of White-crowned Sparrows. If I assume that: 1) the clutch of a White-crowned Sparrow consists of four eggs, each of which weighs 3.3 g when laid (calculated from information in Walsberg and King [1978]), 2) T_e during incubation is 36.8 or 37.5°C (values for eggs of *Z. l. oriantha* in elevated and ground nests, respectively; Zerba and Morton 1983), 3) the temperature of the air in the nest is $T_n - 0.5 = 33.1^\circ\text{C}$ (Kendeigh 1973), and 4) White-crowned Sparrows incubate their eggs 72.7% of each 24-h period (Morton and Carey 1971), then Kendeigh's equation yields a daily cost of incubation that is between 0.193 and 0.230 W in the three races of *Zonotrichia*. These values represent 47–57% of the bird's MR_r and are similar to the values in Table 6 that I calculated for the same races using the h_{wf} of the nest and the minimal T_a s to which incubating female White-crowned Sparrows would probably be exposed.

Estimates of the energetic cost of incubation

based on the nest's thermal conductance will be particularly useful in studies of elevated nests, but of less value for ground nests because they fail to account for the insulation provided by vegetation around the nest and hence overstate the cost of keeping the clutch warm.

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