

# THE INSULATION IN NESTS OF SELECTED NORTH AMERICAN SONGBIRDS

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**ABSTRACT.**—The heat flux ( $Q_n$ ), thermal conductance ( $h$ ), thermal conductivity coefficients ( $k$ ), and density (based on light penetration) of 66 nests representing 11 species of North American songbirds are presented. Well-insulated nests have relatively small values of  $Q_n$  (0.151 to 0.167 W) and  $h$  (3.53 to 3.74  $\text{W m}^{-2} \text{ }^\circ\text{C}^{-1}$ ). The nest wall is either solid or so dense that it prevents light from penetrating it (0 lux<sup>-1</sup>). Poorly insulated nests have relatively high values for  $Q_n$  (0.364 to 0.373 W) and  $h$  (9.95 to 12.35  $\text{W m}^{-2} \text{ }^\circ\text{C}^{-1}$ ), and are exceedingly porous (0.39 to 0.72 lux<sup>-1</sup>). Nests with moderate insulation have values of  $Q_n$  (0.230 to 0.293 W) and  $h$  (4.37 to 6.15  $\text{W m}^{-2} \text{ }^\circ\text{C}^{-1}$ ) that are intermediate in size. Some of these nests are moderately porous (0.0016 to 0.0054 lux<sup>-1</sup>); others are not (0.00002 to 0.0013 lux<sup>-1</sup>). Many facets of the nest (diameter of the entrance; depth, volume, and surface area of the nest cavity; thickness of the nest wall; density of the nest wall) influence  $Q_n$  and  $h$ , but generally weakly. The most important of these is nest density. Values of  $k$  for nests range between 52 and  $239 \times 10^{-3} \text{ W m}^{-1} \text{ }^\circ\text{C}^{-1}$ , but are usually intermediate between those of animal fur and wood. Received 10 December 1979, accepted 4 June 1980.

DURING incubation, the temperature of the clutch is between 34 and 38°C (Huggins 1941, Drent 1975). In order to maintain this narrow temperature range, incubating birds must match the heat lost from the clutch with an equivalent input of heat. The quality of the nest, its location, and its orientation with respect to environmental factors therefore figure importantly in reducing the energetic costs of incubation.

Numerous studies illustrate the significance of the nest site. Many avian species orient their nests to obtain the warmth of the morning sun (Dorst 1962, Hadley 1969, Orr 1970, Riehm 1970, Walsberg and King 1978a). Others situate the nest so that it is shaded during the hottest part of the day, or out of the sun entirely (Maclean 1970). Still others place the nest on the leeward side of vegetation to minimize the impact of wind (Hadley 1969, Schaefer 1976). It is well known that hummingbirds station their nests beneath leaves or overhanging limbs and in so doing appreciably reduce radiational heat exchange with the sky and the sun (Calder 1973a, Southwick and Gates 1975). Cactus Wrens (*Campylorhynchus brunneicapillus*) orient the entrance of the nest so that it faces away from cool winds early in the breeding season, but into warm winds late in the breeding season (Ricklefs and Hainsworth 1969).

Some species also vary the location of the nest in characteristic ways during the breeding season (Nice 1937, Walkinshaw 1944, Horvath 1964, Taylor 1965, Holcomb and Twiest 1968, Ricklefs and Hainsworth 1969) for reasons that are largely unknown. However, in at least one species (the Rufous Hummingbird, *Selasphorus rufus*), the changes ameliorate the microclimate around the nest and have an energy-sparing effect on the incubating female (Horvath 1964).

The quality of the nest is also important in reducing the energetic costs of incubation and conserving heat. Zoogeographical differences in the size and composition of nests illustrate this nicely and have been documented especially well among hummingbirds (Pearson 1953, Wagner 1955, Corley Smith 1969), weaver finches (Collias and Collias 1971), and several Canadian songbirds (Horvath 1963).

Yet, for all of the qualitative information available, there is still very little quan-

titative information about nests in the literature. As Drent (1975: 366) observes, "that nests often provide crucial protection from climatic extremes has perhaps seemed so obvious that little critical research has been done in this area." To our knowledge, there are only four publications in which the insulation of the nest is quantified in physical terms. The earliest is that of Palmgren and Palmgren (1939). These investigators attached nests to the surface of a flask containing hot water and measured how rapidly the water cooled. They discovered differences among the nests of 15 species of European passerines that correlated with the distribution of the birds during the breeding season. For example, Bramblings (*Fringilla montifringilla*), which breed in northern Europe, had more highly insulated nests than congeneric Chaffinches (*F. coelebs*), which breed farther south.

The other three studies appeared more recently. In 1977, Whittow and Berger published a note describing the thermal conductance of four nests of the honeycreeper "Amakihi" (*Loxops virens virens*). In 1978, Walsberg and King contributed two papers dealing with nests of Red-winged Blackbirds (*Agelaius phoeniceus*), Willow Flycatchers (*Empidonax trailii*), and Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*).

To this small collection, we now add new data for the nests of nine more North American songbirds and additional data for two of the songbirds studied previously.

Data such as these are of considerable practical value. Nests are often fixed in composition and can therefore be used by avian taxonomists to separate closely related species (Collias 1964). If the physical properties of the nests are also fixed and different, such a tool may be even more powerful. On the other hand, the composition and structure of nests are strikingly variable in many cases. This variation is the raw material on which natural selection operates to increase a species' breeding range and season (White and Kinney 1974). If we can define the limits of this variation in concrete physical terms, we may be able to predict a priori the ease with which a species can extend its range or breeding season under given climatic conditions.

The quality of the nest also influences the behavioral patterns of nesting birds. White and Kinney (1974), for example, have shown that the nest attendance of Village Weaverbirds (*Ploceus cucullatus*) is inversely related to the insulation of the nest. Riehm (1970) has demonstrated that absences of up to 30 min do not adversely affect the clutch of the Long-tailed Tit (*Aegithalos caudatus*) because the nest cavity is so warmly lined with feathers. Quantitative data on nests may enable us to explain what might otherwise appear to be maladaptive behavior on the part of incubating birds.

Finally, the quality of the nest can significantly reduce the energetic costs of incubation. For example, an incubating Broad-tailed Hummingbird (*Selasphorus platycercus*), one-half of whose body is exposed above the nest rim, expends 41–62% more energy thermoregulating than a female only one-quarter exposed (Calder 1973a). It is estimated that an increase in the thickness of the nest of only 0.05 cm reduces the energy requirements of incubating hummingbirds by 13% (Smith et al. 1974). White-crowned Sparrows in the nest expend 10–11% less energy than conspecifics roosting nearby (Walsberg and King 1978b). We need quantitative information about nests so that we can accurately determine the costs of incubation under prescribed conditions. The point is illustrated by the model of nesting energetics developed by Walsberg and King (1978a,b), in which the thermal conductance of the nest is used to calculate its thermal resistivity.

## METHODS

*Physical relationships.*—We express insulation in terms of the nest's heat flux ( $Q_n$ , expressed in W), which is measured with a heat flux transducer, and thermal conductance ( $h$ , expressed in  $\text{W m}^{-2} \text{ } ^\circ\text{C}^{-1}$ ), which can be calculated from  $Q_n$ , the temperature gradient across the nest wall, and the area of the nest cavity. In addition, we include the thermal conductivity coefficient ( $k$ , expressed in  $\text{W m}^{-1} \text{ } ^\circ\text{C}^{-1}$ ) of the nest. The latter indicates the material to which the nest is comparable in terms of insulation (values of  $k$  are available for many materials including metals, glass, soil, wood, water, human tissue, fur, and air). Thermal conductance values are especially useful for comparing heat flow through unit areas of nests of different species under similar ambient conditions, and for modeling nesting energetics.

Thermal conductance can be calculated using the equation  $h = Q_n/(A)(T_i - T_o)$ , in which  $Q_n$  is the heat flow across the nest,  $A$  is the area of the nest cavity across which this heat flows, and  $(T_i - T_o)$  is the difference between the temperature of the nest cavity and the surface of the nest, respectively.

The thermal conductivity coefficient is more difficult to determine and requires that we make the following simplifying assumptions: (1) the nest cavity is spherical in shape, (2) its walls are uniformly thick, and (3) wall thickness is equal to the thickness of the floor of the nest. These assumptions are subject to more or less error, depending on the nest, but as first approximations they allow us to compute  $k$  by rearranging the equation for conductive heat transfer across a sphere (Birkebak 1966):

$$Q_n = (4\pi)(R_i R_o)(T_i - T_o)(\delta)(k)/(R_o - R_i).$$

$R_i$  is the radius of the sphere of which the nest cavity is a part.  $R_o$  is the radius of the nest (i.e.  $R_i$  + the thickness of the floor of the nest).  $T_i$  is the temperature of the floor of the nest cavity.  $T_o$  is the temperature of the surface of the nest directly opposite the point where  $T_i$  is measured.  $\delta$  is a constant whose size is related to the portion of the sphere across which heat flow takes place: for a hemisphere,  $\delta = 1/2$ ; for any other section of the sphere,  $\delta$  is the surface area of the nest cavity across which heat flow occurs divided by the total surface area of the sphere of which the nest cavity is part.

*Experimental apparatus.*—To measure  $Q_n$ , each nest was suspended from the ceiling of a constant environment chamber (Percival, Boone, Iowa) with 4-ply, 2.54-cm mesh orchard netting (Durex Anti-Bird Mesh, Apex Mills, Inc., New York, N.Y.). The chamber maintained a temperature of  $14.9 \pm 0.3^\circ\text{C}$  ( $\bar{x} \pm \text{CI}_{95}$ ) and was baffled to minimize air flow around the nest. A heat flux transducer (Thermonetics Corp., San Diego, Calif.), with dimensions of  $2.86 \times 2.86 \times 0.16$  cm (length  $\times$  width  $\times$  thickness, respectively) and a constant of  $62.8 \text{ W m}^{-2} \text{ mV}^{-1}$  (calibrated by the manufacturer), was placed on the floor of the nest cavity and connected with a microvoltmeter outside the chamber. The thermal conductivity coefficient of this plate is  $0.20 \text{ W m}^{-1} \text{ } ^\circ\text{C}^{-1}$ . Consequently, the maximum heat flux across it was  $0.66 \text{ W}$  or  $0.44\%$  of the minimal heat flux value that we obtained for the nests. It measured  $Q_n$  directly. The temperature gradient across the nest was measured with thermistors (model 44004, Yellow Springs Instrument Co., Yellow Springs, Ohio) attached to the center of the nest cavity beneath the heat flux plate and to the external surface of the nest directly opposite. An additional thermistor was suspended in the chamber at nest level so that we could monitor chamber temperature for uniformity during each determination of  $Q_n$ . All three thermistors were connected with a 4.5-digit multimeter (model 245, Data Precision, Wakefield, Mass.) outside the chamber.

Our source of heat in the nest cavity was a balloon containing 40 to 70 ml water, depending on the nest. This volume did not visibly distort the nest cavity, although it filled it. The balloon was equipped with a thermistor and a  $1.0 \text{ } \Omega$ ,  $5.0 \text{ W}$  resistor. The latter was the heater and was connected to a power supply, the voltage of which could be varied by hand. Enough power was supplied to the resistor to bring the water in the balloon to  $37^\circ\text{C}$  (approximate incubation temperature; measured by the thermistor) and to maintain it there once steady state was established. Spaces between the balloon and the rim of the nest were filled with small packages of loose insulation and a 2.0-cm lid of styrofoam was then placed on top of the nest.

To determine the area of the nest cavity across which heat was conducted from the balloon, we laid strips of paper in the nest and cut them to fit the exposed surface of the balloon. The area of the strips was obtained later using a planimeter.

A pilot study in which we made several independent measurements of heat flux for the nest of an American Robin (*Turdus migratorius*) indicated that the variation between determinations was small. The  $\bar{x} \pm \text{CI}_{95}$  was  $0.207 \pm 0.058 \text{ W}$ . The coefficient of variation for these determinations was  $10.1\%$ .

*Nest density.*—We quantified the density or weave of the nests in terms of the amount of light that could penetrate them. Each was placed over an opening in the top of a cardboard box. The inside of the

box was otherwise light-tight and painted black. A photometer was mounted on the floor of the box below the opening. An incandescent bulb was then lowered into the nest cavity to a known distance from the photometer.

Light penetration is expressed as the reciprocal of the difference between the light striking the photocell from this distance in the presence ( $L_{np}$ ) and absence ( $L_{na}$ ) of the nest. Because a porous nest permits considerable light to enter the box, the difference ( $L_{na} - L_{np}$ ) is small, but the reciprocal (or light penetration) is large. Conversely, a densely woven nest permits little light to enter the box, ( $L_{na} - L_{np}$ ) is large, and the reciprocal is small. Nests with solid linings were arbitrarily assigned a value of  $0 \text{ lux}^{-1}$  although  $1/(L_{na} - L_{np})$  is not 0.

Light penetration is an admittedly crude measure of nest density and involves factors, such as the absorptivity, reflectivity, and transparency of nest material, that are not directly relevant to the structure's insulation. Nonetheless, this measure of density correlates significantly with the heat flux and thermal conductance of the nests and we present it as an initial method of defining nest density in quantitative terms, which may be refined later.

*Nests.*—We have measured the  $Q_n$  (and from that computed  $k$  and  $h$ ) of 66 nests representing 11 species of North American songbirds. The nests were generally in prime condition, having been obtained during incubation or immediately after the young fledged. The species are the Loggerhead Shrike (*Lanius ludovicianus*), American Robin, Field Sparrow (*Spizella pusilla*), Song Sparrow (*Melospiza melodia*), Mountain and Eastern White-crowned Sparrows (*Zonotrichia leucophrys oriantha* and *leucophrys*, respectively), Rose-breasted Grosbeak (*Pheucticus ludovicianus*), Grey Catbird (*Dumetella carolinensis*), Red-winged Blackbird (*Agelaius phoeniceus*), Northern (Baltimore) Oriole (*Icterus galbula*), and Yellow Warbler (*Dendroica petechia*). All but one of these species has nests that are open bowls, the exception being the oriole. All except the Eastern White-crowned Sparrow (and occasionally the Mountain White-crowned Sparrow) build nests in vegetation above ground.

## RESULTS

The thermal properties of the nests are summarized in Table 1. Nests of Loggerhead Shrikes and American Robins are good insulators, having relatively small values for heat flux and thermal conductance. The nest wall is either solid or so densely woven that it prevents light, and by inference moving air, from penetrating it. At the other extreme are nests of Rose-breasted Grosbeaks and Field Sparrows, which are relatively poor insulators. They have high values for heat flux and thermal conductance and are exceedingly porous. Nests of the remaining species lie between these extremes.

The thermal conductivity coefficients for nests of these 11 songbirds range from  $0.052$  to  $0.239 \text{ W m}^{-1} \text{ }^\circ\text{C}^{-1}$ . These values lie between the coefficients of animal fur ( $0.038$ ) and dry soil ( $0.335$ ). Most of them, however, are between those of animal fur and wood ( $0.126$ ), which suggests that nests are able to trap air for insulation, but not as effectively as fur.

Many facets of the nest's structure appear to influence its heat flux and thermal conductance. These include the diameter of the nest entrance; the depth, volume, and surface area of the nest cavity; the thickness of the floor and wall of the nest; and nest density, as measured by light penetration. Correlation coefficients between these characteristics and  $Q_n$  or  $h$  are generally small (significant values of  $r$  range between  $0.24$  and  $0.71$ ), suggesting that no single factor is responsible for the quality of the nest. The most influential appears to be nest density, for which  $r$  is  $+0.54$  and  $+0.71$  when correlated with  $Q_n$  and  $h$ , respectively ( $P < 0.001$ ,  $df = 61$ ). Nests with high insulation values are not penetrated by light. Those of moderate insulation value usually, but not always (see footnote b in Table 1) allow some light to pass through. Nests with little insulation value barely impede the passage of light.

TABLE 1. Insulation of nests of 11 passerine species.<sup>a</sup>

Species	n	Heat flux ( $Q_n$ ) ( $W \times 10^{-3}$ )	Thermal conductance (k) ( $W m^{-2} \text{ } ^\circ C^{-1}$ )	Thermal conductivity coefficient (k) ( $W m^{-1} \text{ } ^\circ C^{-1} \times 10^{-3}$ )	Light penetration <sup>b</sup> ( $lux^{-1} \times 10^{-5}$ )
Loggerhead Shrike	6	151.44 ± 31.11 a	3.74 ± 0.94 a	65.69 ± 16.04 a	0 a
American Robin	6	168.18 ± 38.06 ab	3.53 ± 0.53 a	70.34 ± 17.46 a	0 a
Red-winged Blackbird	6	229.56 ± 103.37 ab	4.75 ± 1.34 a	79.96 ± 17.88 a	2 (5) a
Mountain White-crowned Sparrow	13	246.69 ± 35.63 b	4.37 ± 0.70 a	76.62 ± 10.93 a	132 a
Song Sparrow	6	257.49 ± 83.23 bc	6.15 ± 1.26 a	96.46 ± 24.12 a	462 (5) a
Northern Oriole	6	258.20 ± 32.74 bc	5.53 ± 0.76 a	70.92 ± 13.15 a	545 a
Grey Catbird	6	258.87 ± 74.44 bc	4.62 ± 1.09 a	92.99 ± 18.30 a	2 a
Eastern White-crowned Sparrow	6	281.90 ± 81.43 bc	4.38 ± 1.24 a	57.36 ± 13.15 a	160 a
Yellow Warbler	2	293.08	4.45	51.79	440 (1)
Rose-breasted Grosbeak	4	364.25 ± 90.02 c	12.35 ± 7.88 b	238.65 ± 108.56 b	39,021 b
Field Sparrow	5	372.63 ± 83.11 c	9.95 ± 2.97 c	88.26 ± 25.20 a	71,722 c

<sup>a</sup> Values in the table are  $\bar{x} \pm CI_{95}$ . Sample size appears in parentheses if it differs from the sample size indicated on the left side of the table. In each column, means *not* followed by the same letter differ at the 0.05 level of significance (Student-Newman-Keuls test). Data for the Yellow Warbler were not included in the analyses.

<sup>b</sup> No light penetrated the nests of 5 of the 6 Red-winged Blackbirds and Grey Catbirds or 8 of the 13 nests of Mountain White-crowned Sparrows.

## DISCUSSION

If the data of Palmgren and Palmgren (1939) are recalculated as thermal conductance values (which requires that one use the area of their flask as  $A$ , initial water temperature as  $T_i$ , and ambient temperature as  $T_o$ ; and translate changes in water temperature into  $W$ ), the nests of 15 European songbirds can be shown to have thermal conductance values between 3.53 and 6.33  $W\ m^{-2}\ ^\circ C^{-1}$ . It should be noted that these investigators measured the insulation of nests that were cooling, rather than under steady state conditions. This method fails to account for the storage of heat by the wall of the nest. Accordingly, our calculations of thermal conductance are only approximations. Nonetheless, the calculated values are similar to the range exhibited by the Amakihi (2.78 to 5.72, Whittow and Berger 1977) and 12 North American forms (3.02 to 4.77, Walsberg and King 1978a,b; 3.53 to 12.35, Table 1). The uniformity is striking given that the measurements were made by four different methods and are for songbirds in widely scattered geographical areas.

Among these species, thermal conductance has been measured on two separate occasions for Mountain White-crowned Sparrows and Red-winged Blackbirds. The similarity for nests of White-crowned Sparrows [4.12 and 4.37  $W\ m^{-2}\ ^\circ C^{-1}$  from Walsberg and King (1978a) and Table 1, respectively] is noteworthy given the fact that the nests of Walsberg and King are from Hart Mountain, Lake County, Oregon (42°30'N, 119°45'W; elevation = 1,890 m), whereas our nests are from Tioga Pass, Mono County, California (38°N, 119°W; elevation = 2,743–3,048 m).

The two values for nests of Red-winged Blackbirds [3.02 and 4.37  $W\ m^{-2}\ ^\circ C^{-1}$  from Walsberg and King (1978b) and Table 1, respectively] are significantly different. Several factors may account for this disparity. Birds studied by Walsberg and King nest in cattail marshes near Pullman, Whitman County, Washington (46°45'N, 117°15'W; elevation = 790 m), whereas our birds nest in weeds, shrubs, and trees bordering reservoirs and lakes in Armonk, Westchester County, New York (41°10'N, 73°40'W; elevation = 118 m). Nest height in Pullman was 51 to 153 cm; in Armonk, 61 to 170 cm. Nests were collected between 20 May and 5 June in Pullman, but between 25 May and 29 September in Armonk. Our nests were collected during incubation and after the young fledged. No information on this point is presented by Walsberg and King (1978b). Any or all of the above factors may contribute to the observed differences among nests in the two studies because (1) the nest cavity of the Red-winged Blackbird is significantly deeper if the nest is 107 cm or more above the ground than it is at lower heights, (2) there is a seasonal change in the nest height of this species, and (3) the young increase the dimensions of the nest during the brooding period (Holcomb and Twiest 1968). It is equally plausible, however, that we have documented real zoogeographical differences between isolated populations of *Agelaius*.

At any rate, the information presented above illustrates some of the factors that influence nest structure and presumably insulation. In some species, we should anticipate considerable variation in nest insulation because the composition or shape of the nest changes during incubation and brooding, either through the activity of the parents (Moynihan 1953, Frith 1956, Krüger 1965, Calder 1973b) or the nestlings (Holcomb and Twiest 1968, Calder 1973b, O'Connor 1975). O'Connor (1975) has pointed out that such changes may be common in species of songbirds with large broods and may be adaptive in that they prevent the young from overheating. If the relationships between nest dimensions and insulation presented above are ap-

plicable to songbirds generally, then alterations in the nest will affect its thermal conductance.

Nest insulation also depends on the materials with which the nest is fabricated [e.g. the correlation coefficient between the thermal conductance and the thermal conductivity coefficient of our nests is  $+0.80$  ( $P < 0.001$ ,  $df = 64$ )]. The selection of materials may in turn depend on what is available and on engineering problems associated with nest placement. Nickell (1958, 1965) has made extensive studies of nest materials and documented differences in nest morphology associated with nest site selection. Schaefer (1976) has recently described similar variations in the nests of Northern Orioles. Many Hawaiian songbirds use wool in the nest when it is available (van Riper 1977). Cliff Swallows (*Petrochelidon pyrrhonota*) select mud with a high sand and low silt content for the nest, whereas Barn Swallows (*Hirundo rustica*) mix grass, hair, and feathers into the mud used for their nests (Kilgore and Knudsen 1977).

The insulating qualities of nests may also depend on where they are found in the field. There are several reports of differences in nest morphology as a function of the nest site. For example, ground nests of the Chinese Thrush (*Garrulax canorus*) are flat and pie-shaped, but nests 2.1 to 4.6 m above the ground are deep bowls with compact walls (van Riper 1973). The nests of Black-billed Magpies (*Pica pica*) are domed when they are built at exposed nest sites, but are open bowls when built in thorn bushes (Linsdale 1937).

Nests are also frequently built for purposes other than heat conservation. For example, the need to thwart nest predation may be of overriding importance. The pensile nests of tropical songbirds with their long tubular entrances are clearly built to discourage predators. Other nests of tropical birds are adapted to shed rain (Collias 1964) and perhaps to dry out quickly. The nest of the Adelie Penguin (*Pygoscelis adeliae*), on the other hand, is apparently adapted to prevent the eggs from being flooded during thaws or buried during blizzards (Sladen 1958). Under these circumstances, the relationships between the thermal quality of a nest and its morphology may be of minimal biological importance.

In summary, the nest represents an evolutionary compromise on the part of a bird between the need to provide a thermally uniform microclimate and safety for the young. Some species can vary the structure of the nest to fit the situation at hand, even to the point of altering it on a day-to-day basis. Hummingbirds, partridge, and megapodes belong in this group. Others are apparently unable to change the structure of the nest, perhaps for genetic reasons, and compensate for deficits in its quality by varying its location or by increasing parental attention. Doves (Russell 1969), some hummingbirds (Horvath 1964), and birds that nest in harsh environments (arctic, insular, and desert forms; Collias 1964) commonly fall into this category. Other species lie somewhere between these two extremes, able to vary the nest and nesting behavior to greater or lesser extents. Quantitative information about nest insulation will be useful in sorting out these reproductive strategies.

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