NEST-SITE SELECTION AND THE RADIATIVE ENVIRONMENT OF THE WARBLING VIREO

GLENN E. WALSBERG

Selection of an appropriate nest site is a critical aspect of avian reproduction, since it determines the environment to which the adult, the eggs, and nidicolous young will be exposed for extensive and critical portions of the life cycle. Thus, nest placement may affect reproductive success importantly, and it presumably has evolved in relation to various factors, such as predation, the local availability of resources, and microclimate.

Although many bird species build open cup nests, few quantitative data are available describing site selection in such forms. In the Sierra Ancha of central Arizona, Warbling Vireos (*Vireo gilvus*) build nests that exhibit characteristics typical of many other species: the nest is a basket-like cup placed in vegetation with no conspicuous tendency for placement in an unusually distinctive microclimate, such as under a sheltering limb (e.g., Calder 1973). For species building such nests, little is known about the role that thermal factors play in determining nest placement. In the following analysis, I document the existence of an inconspicuous but effective form of nest-site selection for thermal advantage in *Vireo gilvus*.

METHODS

Environmental measurements. I studied Warbling Vireo nests and their microenvironments on 4–30 June 1979 in the riparian woodland bordering Parker Creek at an elevation of about 1,500 m in the Sierra Ancha, Gila County, Arizona. Of the 18 vireo nests I examined, 7 were placed in Arizona walnut (*Juglans major*), 5 in Arizona white oak (*Quercus arizonica*), 5 in Arizona sycamore (*Platanus wrightii*), and 1 in Ponderosa pine (*Pinus ponderosa*). These nests were suspended from forked twigs averaging 2.07 ± 0.43 m above ground (range: 1.58–2.92).

The relative contributions of sky and vegetation to the hemisphere over a nest were determined by analyzing hemispherical ("fisheye") photographs taken from 18 nest-sites with the camera axis placed vertically. The fraction of the upper hemisphere occluded by vegetation was calculated for each photograph using the method of Walsberg and King (1978b). Periods of the day when the nest was exposed to direct sunlight were determined by plotting solar paths onto the photographs (Walsberg and King 1978a). Downward short- and long-wave radiation, air temperature, and wind velocity were measured continuously during a seven-day period (June 6–12) during the breeding season of the Warbling Vireo and were averaged by a Campbell Scientific Co. CR5 recorder over one-hour periods. Short-wave radiation was measured in the open using an Eppley pyranometer. Scattered short-wave radiation was measured midway through each hourly period by holding a disc about 20 cm above the sensor surface to occlude direct solar radiation. Direct short-wave radiation was computed as the difference between total and scattered short-wave radiation; direct short-wave radiation perpendicular to the solar beam was calculated using Lambert's cosine law. Long-wave radiation was measured in the open using a Fritschen net radi-

ometer modified as described by Idso (1971). Long-wave radiation from vegetation was calculated using the Stefan-Boltzmann relationship by assuming an emissivity of 0.98 (Gates and Tantraporn 1952) and assuming that vegetation surface temperatures equalled air temperature (T_a), which was measured using a shielded thermocouple 2 m above the ground. Wind velocity was measured continuously at four nest sites using miniature cup anemometers (starting speed about 0.1 m/s).

Physical characteristics of the bird. Long-wave absorptivity and emissivity of the bird were assumed to be 0.98 (Hammel 1956). Short-wave absorptivity of this species' dorsal plumage was measured using a freshly collected specimen at near-normal incidence with a Beckman DK-2A reflecting spectrophotometer. The output from the spectrophotometer was digitalized at 40 nm intervals in the 300–2500 nm wavelength range and integrated with a typical solar spectrum for noon on a clear day at Tempe, Arizona (160 km west and 1,100 m lower in elevation than the field site). Thus calculated, integrated solar reflectivity of the Warbling Vireo's dorsum is 0.73. For an incubating bird, the fractional area (A_p/A_t) of the animal projected on a plane perpendicular to the solar beam was estimated by assuming that the bird approximates a hemicylindrical surface. Depending upon the bird's orientation to the solar beam, A_p/A_t should range from 0.32 to 0.64; the intermediate value of 0.48 was used in all calculations. The characteristic dimension (d) used in estimates of convective heat flow was assumed to equal 0.03 m, the average diameter at midtorso of three Warbling Vireos. An error of 25% in either the estimate of A_p/A_t or d will change the calculated value of the operative environmental temperature 0.3–2.5°C.

Calculations of operative environmental temperature. Meteorological data may be used to estimate the net thermal stress on an animal by applying an operative environmental temperature (=equivalent blackbody temperature) model. The model I use in this analysis has been fully described (Robinson et al. 1976, Campbell 1977), tested by Mahoney and King (1977) and employed in a variety of studies (Walsberg and King 1978a,b, Walsberg and King 1980). Hence, I give here only an abbreviated description.

Operative environmental temperature (T_e) is an integrated measure of an animal's thermal environment and subsumes effects of air temperature and radiation absorbed by the animal. The difference between T_e and body temperature (T_b) defines the thermal gradient between animal and environment. Net heat flux between animal and environment is proportional to this gradient divided by the total thermal resistance of the system. This thermal resistance incorporates both animal and meteorological properties. In the following analysis, I shall calculate the T_e operating on the bird's back as an index of the effect of a shaded nest site upon heat stress acting on the bird.

Statistics. Results are cited as $\bar{x}$ ± S.D. Mean values were compared using a 2-tailed Mann-Whitney U-test.

RESULTS AND DISCUSSION

Analysis of hemispherical photographs indicated that Warbling Vireo nests were situated such that a mean of 2.4 times more sky was visible through the foliage canopy in the eastern portions of the upper hemisphere over the bird than in the western portions of the upper hemisphere (Table 1). Both eastern quadrants of the upper hemisphere were composed of significantly more visible sky than either western quadrant ($P <$

TABLE 1. Percentage of sky visible from nest, by quadrants ($\bar{x} \pm$ S.D., n = 18).

Northeast	30.1 ± 8.1
Southeast	25.7 ± 7.5
Northwest	9.9 ± 4.8
Southwest	13.3 ± 6.5

0.01). This unequal distribution of overhead cover produced 90% more exposure to the solar beam in the morning (32.8 ± 19.8 min) than in the afternoon (17.4 ± 14.3 min); the difference is statistically significant ($P < 0.05$).

The primary thermal factor favoring selection of a nest-site with a much denser leaf canopy in the western half of the overhead cover than in the eastern half probably is not reduction of cold stress during the morning by increased exposure to direct sunlight. Rather, it apparently is amelioration of heat stress during the afternoon by maximizing the time that the nest is shaded. The breeding season of the Warbling Vireo in this portion of the Sierra Ancha is characterized by mild nights and warm days with intense solar radiation (Table 2). Calculations indicate that the combination of warm air temperatures and intense radiation produce operative environmental temperatures averaging as high as 49°C on a nesting bird's dorsum when it is exposed to direct solar radiation (Table 2). For a bird the size of a Warbling Vireo (about 12–17 g), the thermal neutral zone probably extends down to approximately 25°C (estimated using equation 18 of Calder and King [1974] and assuming $T_b = 40°$ C). Due to the insulation added by the nest, this value may be reduced in an incubating individual (Walsberg and King 1978a, b). Thus, during daylight hours an incubating Warbling Vireo is not likely to encounter significant cold stress, even when not exposed to direct solar radiation (Table 2).

In previous studies that documented nest-site selection for thermal advantage in birds that do not use cavities or domed nests, thermally adaptive nest placement generally has been characterized simply by locating nests on thermally favorable sides of trees (e.g., Balda and Bateman 1973) or placement immediately beneath a sheltering structure (e.g., Carpenter 1976). This was not apparent in Warbling Vireos. For

example, of the nests studied, three were located in a quadrant northwest of the trunk of the tree in which the nest was placed, six were in a quadrant northeast of the tree trunk, four were in the southeast quadrant, and five were in the southwest quadrant. Rather, the pattern seen in these vireos is more subtle and similar to that described for White-crowned Sparrows (*Zonotrichia leucophrys*; Walsberg and King 1978a). In these two species, the nest apparently is situated with regard to the vegetation/sky mosaic produced by the plant canopy so as to create a favorable radiative environment. This pattern is not produced solely by the tree or shrub in which the nest is placed, but also by any other overhead vegetation within view of the nest. Such selective placement may not be conspicuous to the casual observer, which may explain why it has not been widely noted. Nevertheless, it may be a relatively common thermoregulatory mechanism used by nesting birds.

LITERATURE CITED

BALDA, R. P. AND G. C. BATEMAN. 1973. The breeding biology of the Piñon Jay. Living Bird 11:5–42.

CALDER, W. A. 1973. Microhabitat selection during nesting of hummingbirds in the Rocky Mountains. Ecology 54:127–134.

CALDER, W. A., AND J. R. KING. 1974. Thermal and caloric relations of birds, p. 259–413. *In* D. S. Farner and J. R. King [eds.], Avian biology, Vol. 5. Academic Press, New York.

CAMPBELL, G. S. 1977. An introduction to environmental biophysics. Springer-Verlag, New York.

CARPENTER, F. L. 1976. Ecology and evolution of an Andean Hummingbird (*Oreotrochilus estella*). Univ. Calif. Publ. Zool. 106:1–74.

GATES, D. M., AND W. TANTRAPORN. 1952. The reflectivity of deciduous trees and herbaceous plants in the infrared to 25 microns. Science 115:613–616.

HAMMEL, H. T. 1956. Infrared emissivities of some arctic fauna. J. Mammal. 37:375–378.

IDSO, S. B. 1971. Transformation of a net radiometer into a hemispherical radiometer. Agric. Meteorol. 9:454–464.

MAHONEY, S. A., AND J. R. KING. 1977. The use of the equivalent black-body temperature in the thermal energetics of small birds. J. Therm. Biol. 2:115–120.

ROBINSON, D. E., G. S. CAMPBELL, AND J. R. KING.

TABLE 2. Mean meteorological data for Warbling Vireos in the Sierra Ancha, Arizona, June 6–12.

Time[1] (local solar)	T_a (°C)	Direct[2] short-wave radiation (W/m²)	Diffuse short-wave radiation (W/m²)	Downward long-wave radiation (W/m²)	Wind velocity (m/s)	T_e (°C) In shade	T_e (°C) Exposed to direct solar beam
6–7	19.8	415	58	318	1.04	19.5	23.9
7–8	26.3	705	80	343	1.26	25.9	33.2
8–9	28.3	710	112	354	1.43	28.1	36.2
9–10	30.1	855	110	364	1.50	30.0	38.8
10–11	29.9	870	109	369	1.10	29.7	40.3
11–12	32.5	901	118	372	1.09	32.2	42.7
12–13	33.0	914	126	373	1.14	32.7	43.2
13–14	33.7	916	132	362	.70	33.5	46.7
14–15	32.8	909	130	368	.58	32.5	47.1
15–16	32.5	860	125	370	.59	32.4	45.8
16–17	30.6	849	103	372	.42	30.3	46.1
17–18	29.1	794	117	374	.22	28.9	49.4
18–19	25.4	332	63	361	.33	25.1	31.9

[1] Values given for daylight hours only.
[2] Irradiance perpendicular to the solar beam.

1976. An evaluation of heat exchange in small birds. J. Comp. Physiol. 105:153–166.

WALSBERG, G. E., AND J. R. KING. 1978a. The heat budget of incubating Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) in Oregon. Physiol. Zool. 51:92–103.

WALSBERG, G. E., AND J. R. KING. 1978b. The energetic consequences of incubation for two passerine species. Auk 95:644–655.

WALSBERG, G. E., AND J. R. KING. 1980. The thermoregulatory significance of the winter roost-sites selected by robins in eastern Washington. Wilson Bull. 92:33–39.

Department of Zoology, Arizona State University, Tempe, Arizona 85281. Accepted for publication 16 July 1980.

NON-RANDOM ORIENTATION OF GILA WOODPECKER NEST ENTRANCES IN SAGUARO CACTI

RICHARD S. INOUYE

NANCY J. HUNTLY

AND

DAVID W. INOUYE

The use of holes for nesting protects birds from harsh weather conditions. Both nest placement and orientation of the entrance may influence the microclimate of the nest. Cactus Wrens (*Campylorhynchus brunneicapillus*), for example, change the orientation of nest entrances in order to gain heat in winter and admit cool air in summer (Ricklefs and Hainsworth 1968). Entrance holes to woodpecker nests in aspen trees in Colorado tend to face directions that receive maximum incident radiation (Inouye 1976). We report here a nonrandom orientation of Gila Woodpecker (*Melanerpes uropygialis*) nest entrances in saguaro cacti (*Cereus giganteus*), and cite some previously unpublished data which support the hypothesis that such orientation serves to reduce energetic costs of nesting birds.

Data on nest entrance orientation were collected (by RSI and NJH) in May 1979 in the Sonoran Desert within the Organ Pipe Cactus National Monument, Pima Co., Arizona. Woodpecker nests were examined in 14 cacti at one site and at 11 cacti at another site. At the second site the two observers, approximately 30 m apart, investigated all saguaros between them in order to reduce any directional bias in sampling. At each nest approximate height of cactus, height of hole, location of hole (in trunk or branch), approximate diameter of hole, and compass orientation were recorded.

Data for nest-hole orientation were corrected to true north, placed in four 90°-quadrats centered on the compass points, and tested for nonrandom dispersion with a χ^2 test. The center of gravity of the nest entrances was calculated by the method of Batschelet (1965).

Data for the two sites were not significantly different. Mean nest entrance orientation for 49 nest holes was 351°. A measure of dispersion, r, varying from 0 to 1.0 was 0.24 (the greater the dispersion the closer r is to 0). Results of χ^2 tests were not significant for the two sites separately, however, the combined data do show a significantly nonrandom orientation ($\chi^2 = 13.0$, $P < 0.01$, 3 df). The circular distribution of nest entrances and their center of gravity are shown in Figure 1.

Mean cactus height for the combined data was 9.6 m ($s = 1.44$, $n = 25$); mean nest entrance height was 7.2 m ($s = 1.5$, $n = 49$). Sample sizes are smaller for cactus height than for entrance holes because some cacti had multiple nest holes.

The orientation of nest entrances in saguaro cacti was nonrandom and centered close to due north, implying a potentially adaptive response to the environment. To support this hypothesis, two criteria must be met: 1) microclimate of the nest cavity must somehow be influenced by the placement and orientation of nests, and 2) this influence must be advantageous to the nesting birds.

Data from Soule (1964) indicate that the summer temperature within a nest is influenced by the orientation of the entrance hole. Temperatures inside north- and south-facing nests were considerably lower than those outside the nests, and north-facing nests were consistently cooler than south-facing nests. Krizman's (1964) data show similar trends for nest cavities in winter.

Nest temperature is undoubtedly important to birds in the nest. Gila Woodpeckers rear a first clutch in May–June and sometimes start a second clutch in July (S. Martindale, pers. comm.). These are the hottest months of the year in southern Arizona and air tem-
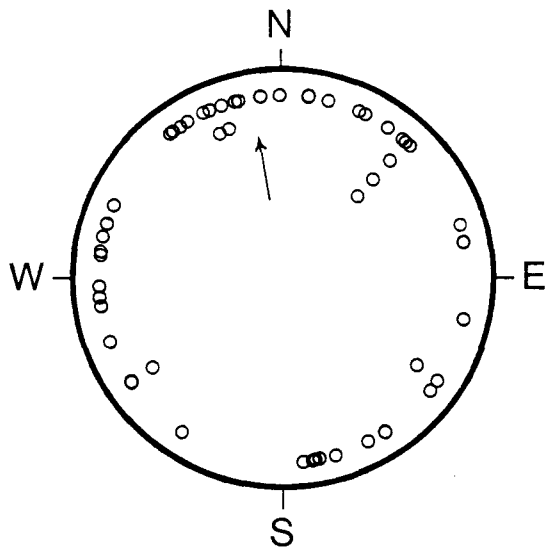

FIGURE 1. Compass orientation of nest entrance holes at two sites in Organ Pipe National Monument, Arizona. Mean direction is indicated by arrow.