

Energy Savings Attending Winter-nest Use by Verdins (*Auriparus flaviceps*)

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The combination of long nights and low temperatures raises the overnight energy requirements of diurnal birds wintering in temperate regions to their highest annual level. The ability of these birds to maintain energy and material balance during this season is challenged further by restrictions on feeding, owing to short day length and reduced food availability. Under such conditions it is not surprising that birds often select roost sites that reduce their heat loss to the environment. These sites include locations within dense foliage (e.g. Gottfried and Franks 1975, Kelty and Lustick 1977, Buttemer 1985), tree cavities (e.g. Knorr 1957, Pitts 1976), and subniveal cavities (e.g. Cade 1953, Sulkava 1969, McNicholl 1979). Verdins (*Auriparus flaviceps*) are unusual among North American birds in that they roost in nests throughout the year. Although these nests vary seasonally in size and extent of nest lining, all are fully enclosed with a small side entrance (Taylor 1971). We report here the energetic consequences of winter-nest use by these birds.

We obtained the 16 Verdins (9 females, 7 males) used in this study from roost sites in a desert wash adjoining the Philip L. Boyd Deep Canyon Desert Research Center in Palm Desert, California. Birds were removed from their nests between 1700 and 2100 PST in late December 1982 and early January 1983. Typically, we collected two individuals on a given evening and transported them to a laboratory at the Center, where they were weighed to the nearest 0.1 g using a triple-beam balance. These birds were then placed individually in metabolism chambers (see below) and usually released the following morning. On several occasions birds were placed in holding cages (1 × 0.5 × 0.5 m) and provided with *Tenebrio* larvae *ad libitum* at the conclusion of the metabolic determinations. Only individuals that gained or maintained body mass while in captivity were used in experiments the second night after their capture.

Standard metabolism was determined by measuring oxygen consumption (\dot{V}_{O_2}) of birds placed individually in one of two 4-l metabolism chambers that had darkened inner surfaces with emissivities near unity (Porter 1969). The only difference between the chambers was that one contained a Verdin winter-

roosting nest whose entrance was appressed to a sealable port on the side of the chamber. Both chambers were immersed in a temperature-regulated water bath that maintained chamber air temperature (T_a) to within $\pm 0.2^\circ\text{C}$ of the desired value. Thermocouples placed in each chamber and through the roof of the nest, extending approximately 1 cm into its interior, permitted monitoring of chamber and nest air temperatures. Fractional oxygen concentrations of the chambers' inlet and outlet air were measured with an Applied Electrochemistry S-3A oxygen analyzer using dry, CO_2 -free air. Oxygen partial pressure within the chambers was maintained above 150 torr by adjusting the flow rate of inlet air between 400 and 600 ml/min over the range of temperatures studied. All \dot{V}_{O_2} values reported are based on measurements that varied by less than 5% for periods longer than 10 min following a 1-h stabilization period. These rates were calculated using Eq. 2 of Hill (1972) and were corrected to standard conditions.

On each evening the first metabolic determination was made no earlier than 2000 and always at T_a 's 15°C or higher. Because Verdins generally entered their roosting nests by 1630, all measurements were made at least 3.5 h after the birds had fed. Following a second determination at a lower T_a , the chambers were withdrawn gently from the water bath and the birds quickly removed. Body temperature (T_b) was recorded within 15 s of removal by inserting a polyethylene-sheathed, 30-gauge thermocouple into the cloaca to a depth where further insertion produced no change in T_b . Each bird was then weighed and placed in the other's metabolic chamber. Metabolic measurements were repeated at the T_a preceding this transfer and followed by a final determination at the initial chamber temperature. Body temperature and body mass of each bird were measured again at the experiment's conclusion. Thus, four \dot{V}_{O_2} measurements were taken nightly for each bird at 2 T_a 's: 2 while it occupied a winter nest and 2 as it slept in an empty metabolic chamber. All conversions of \dot{V}_{O_2} to metabolic heat production assume a thermal equivalent of $20.1 \text{ J/cm}^3 \text{ O}_2$ consumed.

During the course of this study we located 24 winter nests that were occupied by Verdins. We recorded nest heights, tree species used, and nest-entrance orientations. The latter measurements were determined by compass to the nearest 5° and corrected for magnetic variation. Three of the nests were removed in March 1983 to measure the effect of nest orientation on wind penetration. These measurements were carried out in a cylindrical wind tunnel (1.0 m diameter) equipped with diffusers and a variable-speed fan. A

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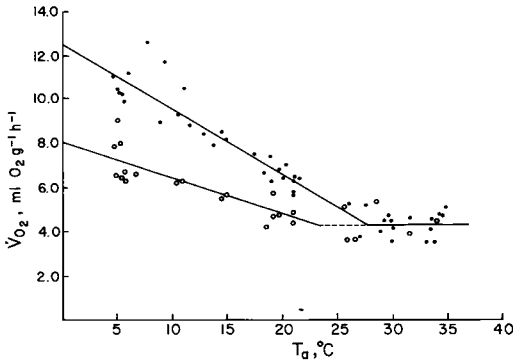


Fig. 1. Rate of oxygen consumption by Verdins inside (open circles) and outside nests (filled circles) as a function of air temperature.

hot-wire anemometer (Thermonetics HWA-103) was inserted through the lower hemisphere of each nest until the sensor rested at a location approximating that of the bird's back (2 cm above the lower interior surface). The nests were positioned centrally in the wind tunnel through attachment to a ring stand. Wind speed in the nest was compared with wind tunnel values of 0.6, 1.6, 2.4, 3.2, and 4.0 m/s for nest-entrance orientations ranging from 30° through 360° to the direction of air flow. The anemometer was held at the same height and orientation for all wind-speed measurements, both with and without the nests. Turbulence intensity in the wind tunnel averaged 0.07 (± 0.02) over the range of wind speeds studied. Values reported are presented as means \pm their standard error.

Metabolic rates measured above 28°C for nest-free birds did not differ significantly from values measured above 25°C for birds in nests. The pooled average ($4.33 \pm 0.13 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$; mean body mass for all physiological measurements was $6.4 \pm 0.1 \text{ g}$) is presumed to represent basal metabolism (\dot{H}_b). This rate is indistinguishable from minimum diurnal values reported for Verdins following a 12-h fast (Goldstein 1974). At each subthermoneutral temperature, however, the \dot{V}_{O_2} of birds occupying nests was lower than that for birds without nests (Fig. 1). At air temperatures lower than 22°C, the relationship of \dot{V}_{O_2} to T_a for nest-free birds was described by the equation:

$$\dot{V}_{\text{O}_2} = 12.56 - 0.299T_a \quad (1)$$

($n = 28, r = 0.91, S_b = 0.026, S_{y \cdot x} = 0.842, \sum x^2 = 1,031.1$).

For Verdins occupying nests, least-squares regression of their \dot{V}_{O_2} as a function of $T_a < 21.0^\circ\text{C}$ yielded:

$$\dot{V}_{\text{O}_2} = 8.11 - 0.167T_a \quad (2)$$

($n = 18, r = 0.84, S_b = 0.026, S_{y \cdot x} = 0.721, \sum x^2 = 742.6$). The slopes of these equations differed significantly from one another (Student's *t*-test, $P < 0.002$). The smaller sample size for Eq. 2 vs. Eq. 1 was due

TABLE 1. Comparison of physiological variables observed or estimated for Verdins with those predicted from allometric relationships for a 6.4-g passerine.

Variable (units) ^a	B		C Predicted ^b	A/C	B/C
	A Verdins inside nest	Verdins outside nest			
\dot{H}_b (mW)	154.7	154.7	142.1	1.09	1.09
$\dot{H}_{m,0^\circ\text{C}}$ (mW) ^c	289.8	448.8	402.1	0.72	1.12
h (mW/°C) ^d	9.7	12.9	12.4	0.78	1.04

^a \dot{H}_b = basal metabolism, $\dot{H}_{m,0^\circ\text{C}}$ = standard metabolism at 0°C, h = heat-transfer coefficient.

^b The allometric equations used to predict values for the variables presented are: $\dot{H}_b = 36.93m^{0.726}$ (after Aschoff and Pohl 1970); $\dot{H}_{m,0^\circ\text{C}} = 149.97m^{0.5513}$ (after Kendeigh et al. 1977); and $h = 5.29m^{0.46}$ (Calder 1974), where m represents body mass in grams.

^c $\dot{H}_{m,0^\circ\text{C}}$ in columns A and B is based on y-intercept values of Eqs. 2 and 1, respectively.

^d h in columns A and B is estimated for $T_n = 5^\circ\text{C}$ and $T_a = 8.8^\circ\text{C}$ (see text for further explanation).

to our discovery that the nest used during initial metabolic measurements consumed O_2 in the bird's absence. The values reported here were taken from a second winter nest that was oven dried at 80°C for 24 h and then rehydrated for 24 h in room air.

These results reveal the energetic benefits of nest occupancy. At an air temperature of 5°C, Verdins have metabolic rates 52% higher when outside than when inside their nests. At the same air temperature, a cavity roost was estimated to confer a 9% reduction in energy expenditure to House Sparrows (*Passer domesticus*; Kendeigh 1961). Although this disparity in energy savings suggests that the roost sites used by House Sparrows are markedly inferior to those used by Verdins, the roosting costs of House Sparrows was inferred from air temperature in the cavity roost and not from direct measurement of the occupant's metabolic rate. In the present study, air temperature in the Verdin winter nest was raised through the bird's metabolic heat production and showed the following relation:

$$T_n = 4.55 + 0.85T_a \quad (3)$$

($n = 24, r = 0.95, S_b = 0.014, S_{y \cdot x} = 0.65, \sum x^2 = 2341.9$),

where T_n and T_a represent air temperature (°C) inside and outside the nest, respectively. From the above equation, air temperature inside the nest would average 8.8°C at an external T_a of 5°C. Although the higher T_a inside the nest will reduce the bird's rate of heat loss, substituting the latter values into Eq. 1 indicates that the energy savings attributable to nest warming amount to only 10%. This implies that the insulative properties of the nest cup are more important than the nest's retention of metabolically warmed air in forestalling heat loss by the roosting bird.

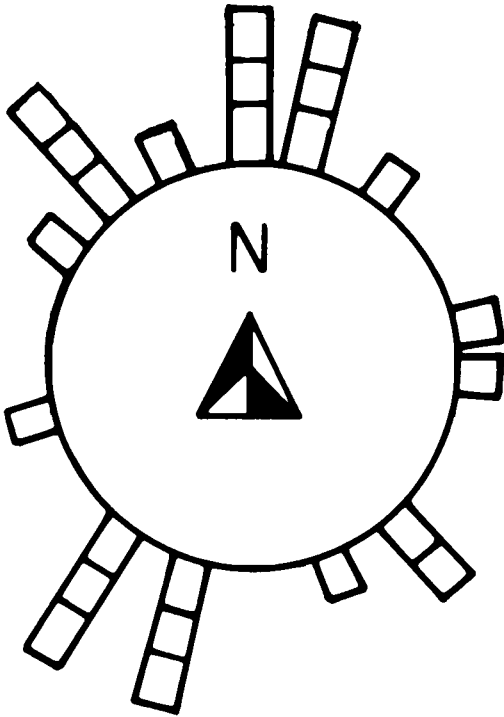


Fig. 2. Nest-entrance orientation of 24 Verdin winter nests (each block represents 1 nest).

A more direct appraisal of the nest's insulative qualities is provided by comparison of overall heat-transfer coefficients (h , in mW/°C) of Verdins for the two sets of measurement. These are calculated from the relation:

$$h = \dot{H}_m / (T_b - T_a), \quad (4)$$

where \dot{H}_m represents the rate of metabolic heat production (in mW), T_b is the bird's core body temperature, and T_a is the air temperature surrounding the bird. Because of the difficulty of removing the metabolic chambers from the water bath without disturbing the birds, measurements of body temperature were restricted to 12 individuals (5 with and 7 without nests) that appeared asleep and did not struggle during T_b measurement. These values, which neither differed significantly between the two groups nor correlated with T_a , averaged 35.7 (± 0.5)°C. Therefore, at a chamber temperature of 5°C, the thermal gradient ($T_b - T_a$) for nest-free birds was 30.7°C, whereas the warmer temperatures inside the nest (Eq. 3) reduce this gradient to 26.9°C. Applying these values to Eq. 4 and assuming a thermal equivalent of 20.1 J/cm³ O₂, the heat-transfer coefficient was 25% lower for birds inside than for those outside the nest. Much of this insulative improvement probably derives from the thermal resistance afforded by the feather-lined nest cup and the tightly woven nest structure un-

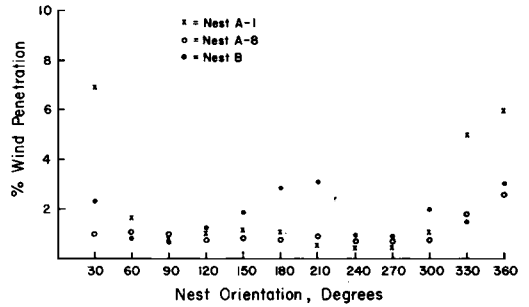


Fig. 3. Percentage of external wind reaching the interior of Verdin winter nests as a function of nest-entrance orientation to the wind. Each point depicts the mean value for external wind conditions producing wind speeds ≥ 0.025 m/s in the nest (see text for details).

derlying the roosting bird (see Walsberg and King 1978). Such properties greatly reduce the energetic liabilities associated with the Verdins' small size (Table 1).

Verdin winter nests were found in four tree species; the most common was *Dalea spinosa* (15 of 24 nests). Three nests each were located in *Acacia greggii* and *Cercidium floridum*, and one nest in *Hyptis emoryi*. The average nest height was 220 ± 15.6 cm and was independent of the tree species used. The orientation of nest entrances for these 24 nests (Fig. 2) was distributed randomly when analyzed for either unimodality ($P > 0.10$; Ajne's second test in Batschelet 1972) or multimodality ($P > 0.05$; Rao's test in Batschelet 1972). This pattern has been noted for winter nests of other Verdin populations (Taylor 1971, Austin 1976).

In contrast to the random orientation of winter-roost nests, a significant proportion of Verdin breeding nests constructed in early spring are directed away from the prevailing wind direction, and the majority of those constructed later in the summer are oriented into the wind (Austin 1976). Furthermore, fledging success was significantly greater in nests oriented in the predominant wind direction. Austin (1976) attributed this to the thermal amelioration attending wind avoidance during the early, cooler, breeding period and, conversely, to enhancement of convective cooling later in the breeding season when temperatures are higher.

Given these implications, we were somewhat surprised at the limited effect nest orientation had on wind penetration into the nest (Fig. 3), although this may reflect seasonal differences in nest construction. For the three nests studied wind penetration averaged less than 5% when nest entrances were oriented between $\pm 30^\circ$ to the direction of wind. Measurements taken for all other orientations (i.e. 60–300°) displayed average values of less than 2%, although one nest

(nest B) displayed considerable variation throughout this range (Fig. 3). Air penetrance by ambient wind to the nest interior actually would be lower in the field, because our measurements lacked the conference of wind attenuation provided by the tree supporting each nest.

Nest occupancy under windy conditions would provide Verdins even greater energy savings than the laboratory measurements indicate. From studies of wind effects on metabolic heat production of small birds (Robinson et al. 1976, Buttemer 1981, Walsberg 1986), heat loss of Verdins exposed to a wind speed of 1.5 m/s (5.4 km/h) at an air temperature of 10°C should be at least 25% greater than that of birds in still air.

Assuming wind penetration through winter nests averages 2% (Fig. 3) and a roost period of 14.5 h, we can compare estimates of overnight energy expenditure for Verdins occupying winter nests with those of exposed birds under low wind and still air conditions. At an average overnight T_a of 10°C (average overnight low T_a 's were $7.8 \pm 0.5^\circ\text{C}$ in January 1983; A. and V. Muth pers. comm.) and an average wind speed of 1.5 m/s, an exposed bird would expend at least 22.3 kJ (from Eq. 1). In contrast, because the wind speed inside winter nests (0.03 m/s) is insufficient to promote forced convective heat transfer (Gates 1980), the roosting cost for a Verdin using a nest would be the same as under still-air conditions, or 12.0 kJ (from Eq. 2). If the air temperature inside the nest or, more important, the thermal gradient through the lower portion of the nest were affected by a wind speed of 1.5 m/s, the actual cost might be somewhat higher. Under wind-free conditions and an air temperature of 10°C, exposed birds would expend 49% more energy than those in nests, as overnight expenditures at the two sites would be 17.8 and 12.0 kJ/bird, respectively. Under clear atmospheric conditions the relative energy savings attending nest use would be even greater because of increased radiative heat losses from exposed birds. Although we lack sufficient information to evaluate this effect, nocturnal radiant sky temperatures average 18° lower than T_a at this season in the Sonoran desert (Walsberg 1986).

From the above comparisons, it is clear that Verdins' overnight energy expenditures are substantially reduced through use of winter nests. Such benefits are especially important for small birds because of size limitations on fasting endurance (Calder 1974). Although Verdin body composition has been studied during spring (Austin 1971), there are no data for winter populations. Assuming winter energy reserves are proportionate to those of similar-size Golden-crowned Kinglets (*Regulus satrapa*; Blem and Pagels 1984) and that 0.1 g of extractable lipid is unavailable for thermogenic needs (Newton 1969), Verdins would enter their winter roosts with only 21 kJ of stored energy. Without their use of winter nests, survival would be challenged by combinations of ep-

isodic occurrences of low nocturnal temperatures, high winds, and restricted food availability.

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The Center-edge Effect: The Result of a War of Attrition Between Territorial Contestants?

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Resident birds often respond more intensely to simulated intrusions at the center than at the edge of their territories [the center-edge (CE) effect; Falls 1982]. Very few hypotheses have been proposed to account for the ecological significance of the effect. Explanations of the CE effect are of two types. First, the intruders are more likely to be closer to residents in the center than at the edge of the territory. It follows that if a resident's response is graded as a function of the distance to the opponent (and not position on the territory), CE effects may be the result of proximity between contestants rather than of the intruder's location on the territory. A second type of explanation argues that the center of a territory has a higher value to a resident than the periphery. We examined the ways territory centers might be more valuable than the periphery and used game theory to generate predictions for each hypothesis. We tested the predictions against data from an exhaustive review of the literature on avian territorial defense.

The intensity of a resident's response to intrusion can vary continuously from mild through intense threat displays, to outright violence. Territorial contests can be analyzed in terms of a war of attrition (Parker 1984). In a war of attrition with no informa-

tion about opponents (Bishop et al. 1978), the evolutionarily stable strategy is to choose a persistence time based on the ratio V/K , where V is the value of winning and K the rate at which costs can be expended during the contest (Parker 1984). We assumed that the intensity of an individual's response denotes its evaluation of V/K , an assumption supported by Enquist et al. (1985), Ewald and Orians (1983), and Krebs (1982).

The rate at which costs are expended (K) during a contest is set by an animal's resource holding potential (RHP). RHP is not likely to explain the CE effect because, although an individual's RHP can change slowly over time, there is no reason to expect it to change with position on the territory. On the other hand, there are three ways the value of winning (V) can change with the distance from the territory center to the location of the contest. In the *strategic-center hypothesis*, losing possession of the center of a territory more likely leads to loss of the whole territory than does forgoing an equivalent surface at the periphery. The center therefore has a higher strategic value than the periphery. Because all territories have centers, the CE effect should be a characteristic of all territorial defense. In the *central-place foraging hypothesis*, many birds feed their young with food collected on their large territories. If birds defend exclusive access to food resources located around a central nest, then the value of winning exclusive access declines with distance from the territory center. This is because the rate of food delivery to the nest declines

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