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## RELATION OF METABOLISM TO AMBIENT TEMPERATURE IN THE VERDIN

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The Verdin (*Auriparus flaviceps*) is an inhabitant of the Warm Desert of North America. The species is mainly insectivorous and diurnal and thus is exposed to maximal desert temperatures. As nonmigratory residents, Verdins must also endure the low temperatures of winter nights.

Verdins are among the smallest passerines in North America. Birds used in this study averaged 6.8 g ( $n = 10$ , range, 6.2-7.35 g). This small size and concomitant high surface-to-volume ratio accentuate problems of temperature balance and metabolic stress.

Lasiewski and Dawson (1967), in their summary of the literature on oxygen consumption in birds in relation to environmental temperature, give data for few species as small as Verdins and no data at all for an insectivorous inhabitant of temperate deserts. More recent studies have added some information (e.g., Mugaas and Templeton 1970), but they have not filled this gap.

### MATERIALS AND METHODS

This study was conducted between 27 April and 29 May 1968. The birds collected for the study were from an area 6 miles E of Las Cruces, Doña Ana County, New Mexico. The dominant plants in this area, a slowly sloping mesa at the foot of the Organ Mountains, are creosotebush (*Larrea divaricata*), white thorn (*Acacia constricta*), range ratany (*Krameria parvifolia*) and, along the numerous arroyos where the Verdin nests, apache plume (*Fallugia paradoxa*), little leaf sumac (*Rhus microphylla*), and desert willow (*Chilopsis linearis*). For a more detailed description of this area and the ecology of resident Verdins, see Singh (1964), Moore (1965), and Raitt and Maze (1968).

The birds were collected on their nests approximately 1 hr after sunset. They were maintained in the dark overnight, allowing the experiments to be run with birds in a 12-hr post-absorptive condition.

An open-flow system was used. It consisted of a vacuum pump which passed the air through a column of Drierite (calcium sulfate) and a column of As-

carite to remove moisture and carbon dioxide. The air was then passed through the animal chamber, using a 308 × 85 mm plexiglass tube. Air entered the chamber through one end of the tube and exited through the other at a mean rate of 7.25 liters/hr ( $n = 35$ , range, 6.72-7.88 liters/hr, SD = 0.25). The bird rested on a wire mesh screen suspended 20 mm above the bottom of the chamber, over a layer of mineral oil. The chamber itself was housed in a darkened incubator. Air leaving the chamber passed through a second set of Ascarite and Drierite columns, through a wet test flow meter, and then through a F1100 Roger Gilmont meter into a Beckman E2 oxygen analyzer, on which oxygen percentages were recorded. Chamber temperatures were monitored by a Yellow Springs telethermometer.

Two sets of temperature groupings were utilized in the experiments with five birds in each set. With each bird in the first group, the ambient temperature was set at 20°C and then lowered systematically to 15°C and 10°C. All birds in this group died at temperatures below 10°C. In the second group the ambient temperature was started at 25°C and then raised to 30°C, 35°C, and 40°C. In each group the individual birds were allowed to remain at the experimental temperature for one hour before readings began. Readings were taken at 10-min intervals throughout the second hour. Oxygen consumption values (corrected to STP) used for analysis were based on the last two readings at each temperature and calculated by equation 5 of Depocas and Hart (1957).

### RESULTS

Oxygen consumption results for the birds are summarized in figure 1. In order to find the line of best fit, a curvilinear regression line was plotted via a second-degree polynomial orthogonal comparison for equally spaced treatments (Steel and Torrie 1960: 222-229). This method was used because the data suggested a parabolic pattern. It was possible to use the orthogonal method because the readings were taken at 5-degree intervals. The formula of the parabola is  $y = 11.1541 - 0.4550x + 0.0076x^2$ , where  $y$  equals predicted ml O<sub>2</sub>/g-hr and  $x$  equals ambient temperature. The values for the respective points falling on the line are: 7.37 ml/g-hr at 10°C; 6.07 ml/g-hr at 15°C; 5.09 ml/g-hr at 20°C; 4.53 ml/g-hr at 25°C; 4.34 ml/g-hr at 30°C; 4.53 ml/g-hr at 35°C; 5.11 ml/g-hr at 40°C.

Since it is impossible to have the birds remain completely without movement during an experiment of this type, the metabolic values obtained are measures of standard metabolism rather than basal metab-

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TABLE 1. Analysis of variance for oxygen consumption of Verdins.

	Degrees of freedom	Sum of squares	Mean square	F value
Total	34	65.3167		
Treatment <sup>a</sup>	6	41.6269	6.9378	8.1997 <sup>b</sup>
Linear	(1)	19.9056	19.9056	23.5363 <sup>b</sup>
Quadratic	(1)	15.2724	15.2724	18.0503 <sup>b</sup>
Deviation	(4)	6.4489	1.6122	1.9054 n.s.
Error	28	23.6898	0.8461	

<sup>a</sup> Variation between temperature treatments.

<sup>b</sup> Significant at the 0.05 level.

olism. The oxygen consumption rate of 4.34 ml/g-hr is the standard metabolic rate (SMR) at its lowest point (30°C) as obtained from the curvilinear regression (fig. 1).

To recognize a thermal neutral zone—the temperature range over which metabolic rate does not differ significantly from the SMR—an analysis of variance was used (table 1). The F-test and a least significant difference (LSD) test indicated that the results at 10°C and 15°C were significantly different from all the others, but that none of the other results was significantly different from any other. The thermal neutral zone would appear to be 20°–40°C; however, birds exposed to 40°C died within a few hours after removal from the animal chamber. It is therefore difficult to put an upper limit on the zone of thermal neutrality, but it seems advisable to accept 20°–35°C as the approximate limits of the zone.

## DISCUSSION

**Metabolism.** In dealing with the meaning of the oxygen consumption data for the Verdin, a problem is presented by the lack of such data on any other small, nonmigratory, insectivorous bird inhabiting a desert. The SMR (4.34 ml/g-hr) obtained for the Verdin is 97% of the value expected from the equation relating SMR and body weight in passerines obtained by Lasiewski and Dawson (1967), and 114% of the value expected from the equation for birds below 100 g obtained by King and Farner (1961).

It should be noted that the SMR value obtained from this study may be elevated due to the stresses of prolonged fasting, general handling, and, in the case of lower ambient temperatures, the fact that the birds used were “spring” birds. The effect of the latter might be presumed to be minimal on the basis of studies on two other bird species which found that conductance and metabolism do not significantly change seasonally (Hissa and Palokangas 1970; Mugaas and Templeton 1970).

**Conductance.** For purposes of comparing thermal conductance (C) data, I calculated the linear regression of the metabolic rates below the lower limit of thermal neutrality (20°C) for the Verdin. This resulted in a line represented by the formula  $y = 9.27 - 0.20x$ , where  $y$  equals the rate of oxygen consumption and  $x$  equals the ambient temperature. The slope of this line then represents C expressed as ml O<sub>2</sub>/g-hr-°C (the higher the value, the greater the thermal conductance and the less effective the insulation). A relationship between body weight and thermal conductance has been demonstrated in hummingbirds (Lasiewski 1963) and small mammals (Scholander et al. 1950). Lasiewski et al. (1967) ex-

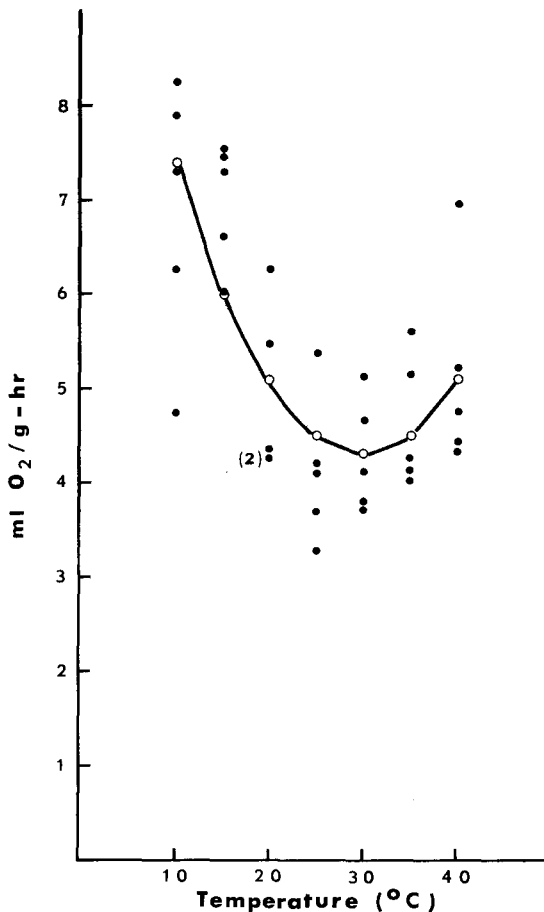


FIGURE 1. Oxygen consumption at various ambient temperatures for the Verdin. Closed circles represent actual data for each bird. Open circles represent the points obtained from the equation for the orthogonal regression,  $y = 11.1541 - 0.4550x + 0.0076x^2$ , where  $y = \text{ml O}_2/\text{g-hr}$  and  $x = \text{ambient temperature } (^\circ\text{C})$ .

pressed this relationship for birds by the equation  $C = 0.848W^{-0.508}$ . Comparing the value obtained for the Verdin with that expected from this equation indicates a relatively low rate of conductance, 62% of the expected.

**Ecological implications.** Yarbrough (1971) has utilized standard metabolic data, thermal conductance, and other energetic parameters to analyze the role that distribution and ecology play in thermoregulation in small birds. Table 2 summarizes some of these parameters for the Verdin and three other species selected from the literature. In his discussion of metabolism, Yarbrough stated that except for species with exceptionally high values of C or very small size, such as the Black-rumped Waxbill (*Estrilda troglodytes*), tropical and desert species have reduced metabolic rates as compared to the King-Farner equation. Not only does the Verdin not have a reduced SMR, but, as in the temperate Red-breasted Nuthatch (*Sitta canadensis*) and Great Tit (*Parus major*), the rate appears to be amplified (table 2). Similarly, the Verdin's C is greatly depressed from its expected value. These two factors would indicate that this

TABLE 2. Metabolic data for selected bird species.

Species	Weight (g)	SMR <sup>a</sup> ml O <sub>2</sub> /g-hr	SMR% <sup>b</sup>	C <sup>a</sup> ml O <sub>2</sub> /g-hr-°C	C% <sup>c</sup>	Source
Verdin	6.8	4.34	114	0.2	62	Present study
Black-rumped Waxbill	6.1	3.5	90	0.4	118	Lasiewski et al. 1964
Red-breasted Nuthatch	11.2	3.71	116	0.2	80	Mugaas and Templeton 1970
Great Tit	18.97	3.5	112	0.24	126	Hissa and Palokangas 1970

<sup>a</sup> SMR = standard metabolic rate; C = thermal conductance.

<sup>b</sup> SMR% = (SMR/7.29W<sup>-0.341</sup>) × 100, M<sub>b</sub>% of Yarbrough (1971).

<sup>c</sup> C% = (C/0.848W<sup>-0.508</sup>) × 100 as in Yarbrough (1971).

species is physiologically adapted to live in cooler temperate climates.

Extensive interpretation of the Verdin's thermoregulatory mechanism at high ambient temperatures is difficult in the absence of body temperature data; however, it seems apparent that increased SMR would increase water loss and that this additional physiological parameter would be detrimental to a xerophilous species. One possible strategy by which this water loss might be reduced would have the bird being capable of experiencing periods of hyperthermia. This seems unlikely in light of the fact that the birds subjected to 40°C died. An alternative strategy would enable the bird to avoid environmental extremes by modifying its habitat. Small domed nests are maintained by the species and used all year round, separately, by both sexes (Moore 1965; Taylor 1967). During the breeding season the males maintain roosting nests. It is possible that this small nest may afford the species protection against dehydration by buffering temperature and humidity during the summer months.

Conservation of energy derived from roosting in a nest box during cold weather has been demonstrated by Kendeigh (1961) for the House Sparrow (*Passer domesticus*). In the hole-nesting Red-breasted Nuthatch, utilization of nest boxes on cold nights has been observed (Mugaas and Templeton 1970), although its roosting habits in nature are not described. Cases of Verdins that were found in good condition within ice-covered nests have been reported (Bent 1946; Moore 1965; Taylor 1967) and tend to lend credence to the hypothesis that these nests act as a buffer against temperature and inclement weather for this species.

Collias (1964) suggests that hole-nesting may have evolved in north temperate birds as a protection for altricial young and that closed nests probably evolved among tropical birds as a protection against rain and predators. The origins and relationships of the Verdin are uncertain (Taylor 1970a,b), but whether they evolved from northern hole-nesting ancestors or from tropical ones that built closed nests, it seems likely that the present adaptive significance of their nests lies largely in the protection against extremes of temperature and humidity.

To understand more fully the extent of modification of microclimate by the nest, year-round field observations of humidity and temperature are needed. This was attempted during the present study, but proved unsuccessful in the absence of constant recording equipment.

#### SUMMARY

Responses of oxygen consumption in the Verdin to ambient temperature were studied in the laboratory.

The standard metabolic rate (SMR) for the species was found to be 4.34 ml O<sub>2</sub>/g-hr. This value is higher than expected based on the King-Farner equation. The approximate limits of the difficult to define thermal neutral zone are 20°–35°C. The thermal conductance value (C) obtained from the linear regression below 20°C was 0.20 ml O<sub>2</sub>/g-hr-°C. This is lower than the value expected from the equation relating conductance to size. Increased SMR and decreased C suggest that the Verdin is physiologically adapted to live in the cool ambient temperatures of the North Temperate Zone deserts which it inhabits.

#### ACKNOWLEDGMENTS

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## WHITE-WINGED JUNCO IN TEXAS

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On 19 December 1968 I collected an immature male White-winged Junco (*Junco hyemalis aikenii*) at Quitaque (5.75 miles N, 3.5 miles W), Briscoe County, Texas. This appears to be the first record of this race for the state. The bird was alone in a dense stand of oaks (*Quercus* sp.) and junipers (*Juniperus* sp.) on the floor of the canyon of the Little

Red River. The specimen has been deposited in the National Museum of Natural History (No. 531924).

The appearance of the White-winged Junco in Texas is overdue, for it occurs in winter in adjacent areas of northeastern New Mexico (Hubbard, *New Mexico Ornithol. Soc. Publ.*, No. 3:95, 1970) and western Oklahoma (Sutton, *Oklahoma birds*, Univ. Oklahoma Press, Norman, p. 618, 1967). The taxonomic status of various forms of *Junco* is a matter of debate. I follow the Thirty-second Supplement to the A.O.U. Check-list (*Auk* 90:411-419, 1973) in treating *aikenii* as a race of *J. hyemalis*.

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