THERMOREGULATION IN THE RED-BREASTED NUTHATCH (*SITTA CANADENSIS*)

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The effects of temperature on metabolism and evaporative water loss in several species of small birds (weighing less than 15 g) have already been examined. Data for the Zebra Finch, *Taeniopygia castanotis* (Calder 1964; Cade et al. 1965), the Black-rumped Waxbill, *Estrilda troglodytes* (Lasiewski et al. 1964; Cade et al. 1965), and the House Wren, *Troglodytes aedon* (Kendeigh 1939), show that these birds have lower critical temperatures which range from 28 to 38°C. Such high lower critical temperatures reflect high rates of thermal conduction (Scholander et al. 1950). Because these birds are either resident in or migrate to warm areas, high rates of thermal conduction would be an advantage in aiding heat loss.

Similar responses of small birds which are continuous residents in the subarctic and north temperate zones have been little studied. This group is faced with a wide range of ambient temperatures over which they must maintain homeothermy. Because insulation is limited by body size, the maintenance of an energy balance must become a problem, especially in the winter when foraging time diminishes and heat production increases. Alaskan Hoary, *Acanthis hornemanni exilipes*, and Common Redpolls, *Acanthis flammea flammea* (Brooks 1968), cope with these problems by having a high rate and quantity of gross energy intake at low temperatures, by selecting high-calorie foods, by increasing their digestive efficiency at extreme low temperatures, by possessing plumage with greater insulative value than the plumage of migrants and southern residents, and by continuing activity at very low light intensities.

Red-breasted Nuthatches (*Sitta canadensis*) resident in certain coniferous forest areas of western North America also face yearly extremes of temperature and photoperiod. Their range extends as far north as Anchorage, Alaska, in the west and James Bay and Newfoundland in the east, and as far south as southern California, southeast Arizona, and southcentral Colorado in the west, and eastern Tennessee and western North Carolina in the east. Populations at high latitudes and altitudes may migrate erratically and records indicate they occur occasionally during the winter as far south as southern Arizona, southern New Mexico, Texas, southern Louisiana, southern Mississippi, and northern Florida (A.O.U. 1957). In the study area near Missoula, Montana, these birds may encounter air temperatures ranging from –40 to 38°C during their yearly cycle (pers. comm.; Bakus 1959). Metabolism and evaporative water loss, therefore, were examined in the Red-breasted Nuthatch at various temperatures during the summer and winter to determine if seasonal changes occurred.

MATERIALS AND METHODS

Oxygen consumption was monitored with a Beckman G-2 paramagnetic oxygen analyzer in an open flow system, and data were recorded on a Brown single strip recorder. The instrument was routinely calibrated and standarized using dry air at 20.93 per cent O_2 for a zero gas and 12 per cent O_2 in N_2 as a span gas. The flow system was designed to allow measurement of oxygen consumption, evaporative water loss, and carbon dioxide production, singly or simultaneously.

A small aquarium pump provided the air flow which passed in succession via "Tygon," copper, and glass tubing connections through (1) a train of chemical absorbents for the removal of water and carbon dioxide from the air, (2) a coil of copper tubing within the temperature cabinet, (3) a darkened metabolism chamber, (4) a system of U tubes of silica gel and "Ascarite" for analysis of water and carbon dioxide, respectively, and (5) the oxygen analyzer which was vented to the atmosphere.

Flow rates through the metabolism chamber were maintained at a constant level of 628 cc air/min (uncorrected to STP) in all but the first six oxygen consumption tests, which were conducted at a constant flow rate of 320 cc air/min (uncorrected to STP). For each test the pressure in the metabolism chamber was kept constant at a gauge pressure between 6 and 12 mm Hg, giving the chamber an absolute pressure between 670 and 690 mm Hg. After removal of the water vapor and carbon dioxide

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from the post metabolism chamber air flow, an aliquot of it was diverted through a calibrated rotameter and into the analyzer at precisely 150 cc air/min. The remainder was discarded to the atmosphere.

The freezer portion of a refrigerator converted into a controlled temperature cabinet was capable of holding a constant temperature (± 0.5°C) for tests conducted between –16 and 43°C. To achieve temperatures for tests below –16°C, dry ice was placed in the cabinet. These very low temperatures were constant to only ± 1°C. The metabolism chamber was fashioned from a new 1-gal paint can. Its lid was equipped with an inlet port extending two-thirds of the way into the can, an outlet port, and an air tight coupling for a thermistor probe. A 0.5-inch mesh wire screen, equipped with a perch, held the bird about 1.5 inches from the bottom of the can. A 0.2-inch layer of mineral oil covered the bottom of the can and served to trap the urine and feces eliminated by the bird. Periodic tests using an empty metabolism chamber indicated that there were no leaks or water vapor in the apparatus.

The 19 experimental birds were captured near Missoula, Missoula County, Montana, in traps of the type described by McCowery (1961). The birds were banded for identification and, after a short (1–2 day) period of adjustment, placed in a 6 × 6 × 9 ft outdoor flight cage. The outdoor cage had a waterproof roof, but its sides were covered with window screen so the birds were exposed to the natural photoperiod and weather conditions of the Missoula area. The birds remained in the outdoor flight cage for two or more weeks before being tested, and most gained about 1 g body weight on an ad lib. diet of suet, raw spanish peanuts, a peanut butter bacon-fat mixture, and 20–30 meal worms (*Tenebrio molitor*) per bird per day. These birds, both in the wild and captivity, utilized snow as a water source in the winter. Birds showing signs of molting or a weight loss of more than 2 g were not tested.

All the tests in this experiment were conducted between 09:00 and 18:00. At about 21:00 the night before a test, the bird was taken from the outdoor cage and put to roost in a small cage in the laboratory. Food and water were available ad lib. This system of handling produced a minimum of disturbance to the bird and, in the winter, insured a minimum loss of stored energy prior to testing. After the test period the bird was returned to the outdoor cage and not tested again for 3–7 days. The summer tests were conducted 25 July–23 September 1966, and the winter tests, 6 January–6 February 1967.

The birds were weighed to the nearest 0.01 g before and after each test period. At temperatures from –16 to 39°C, test periods were 6–9 hr. By starting with a low temperature and, after a minimal record was obtained, changing to a temperature 10–20°C higher, two determinations of oxygen consumption were conducted for each test period. The bird was not removed from the metabolism chamber during the 30-min interval required for temperature change. At temperatures from –30 to –17°C and from 40 to 43°C, test periods did not exceed 2.5 hr and yielded one determination of minimal oxygen consumption at one particular temperature per test period. By following this procedure, four or five separate values of oxygen consumption were determined for each bird over the entire temperature range. Only those lowest values constant over a period of at least 2 min were selected for calculating oxygen consumption. In many cases constant values were obtained for periods exceeding 20 min. The rate of oxygen consumed per gram body weight per hour at STP was calculated, using conversion factors and equation 10 of Depocas and Hart (1957).

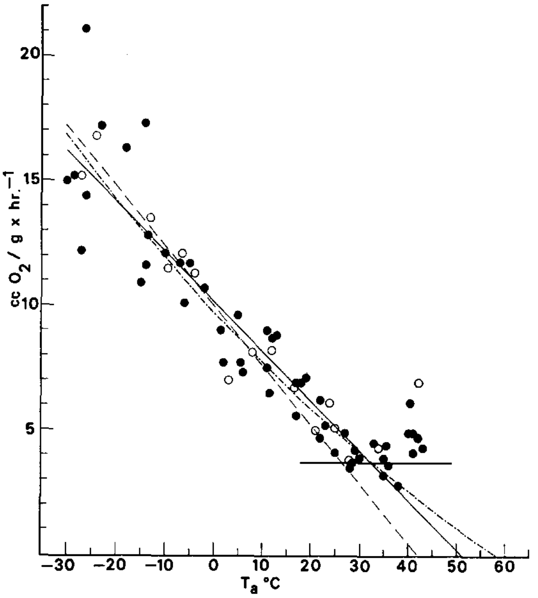

FIGURE 1. Oxygen consumption of 19 Red-breasted Nuthatches as a function of ambient temperature (T_a°C). Closed and open circles represent summer and winter birds, respectively. For summer and winter values combined, the solid line is the linear regression, and the broken line the curvilinear regression. The dashed line represents the best eye-fitted regression extrapolating to zero metabolism at body temperature. The horizontal line represents the average resting metabolic rate.

When animals were minimally consuming oxygen, air from the outlet port was diverted for 20-min intervals through three U tubes each of silica gel and "Ascarite" for the gravimetric determination (to the nearest mg) of evaporative water loss and carbon dioxide production, respectively. If oxygen consumption did not remain minimal during this interval, the carbon dioxide and water data were rejected. Evaporative water loss was measured only at temperatures above 0°C. The ratio of heat lost to heat produced (the e/p ratio) was calculated assuming a caloric equivalent of 4.8 kcal/liter for the oxygen consumed and a heat of vaporization of 0.58 kcal/liter for the water loss. The weight of carbon dioxide was converted to a volume using the conversion 1.000 g = 1.977 liter at STP.

Regression lines of oxygen consumption and carbon dioxide production were calculated for both summer and winter birds. These lines were then statistically compared (summer vs. winter in each case), using Student's *t* test.

RESULTS

OXYGEN CONSUMPTION

The Red-breasted Nuthatches used in this study weighed 9.8–14.2 g (mean = 11.2 g).

TABLE. 1. Regression line formulas for increasing oxygen consumption between 35 and -30°C.

Season	Regression line formulas where y = cc O_2($g \times hr)^{-1}$ and x = the ambient temperature (°C).	Standard error of estimate	n
Summer	$y = 10.21 - 0.20x$	1.59	47
	$y = 9.96 + 0.00062x^2 - 0.21x$	1.59	47
Winter	$y = 10.19 - 0.21x$	1.05	15
	$y = 9.79 + 0.0012x^2 - 0.22x$	1.01	15
Summer and winter combined	$y = 10.20 - 0.20x$	1.47	62
	$y = 9.92 + 0.00074x^2 - 0.21x$	1.45	62

In both summer and winter their oxygen consumption increased with decreasing temperature from about 35 to -30°C with no indication of a well defined lower critical temperature (fig. 1). Linear and curvilinear regression lines calculated for the oxygen consumption values between these temperatures are given in table 1.

Mean oxygen consumption between 33 and 38°C was 3.71 cc O_2($g \times hr)^{-1}$, the equivalent of 4.78 kcal/bird per 24 hr, and was taken to best represent resting metabolism within this poorly defined thermoneutral zone.

Oxygen consumption rose with increasing temperatures above 40°C to values of 4.2–7.0 cc O_2($g \times hr)^{-1}$.

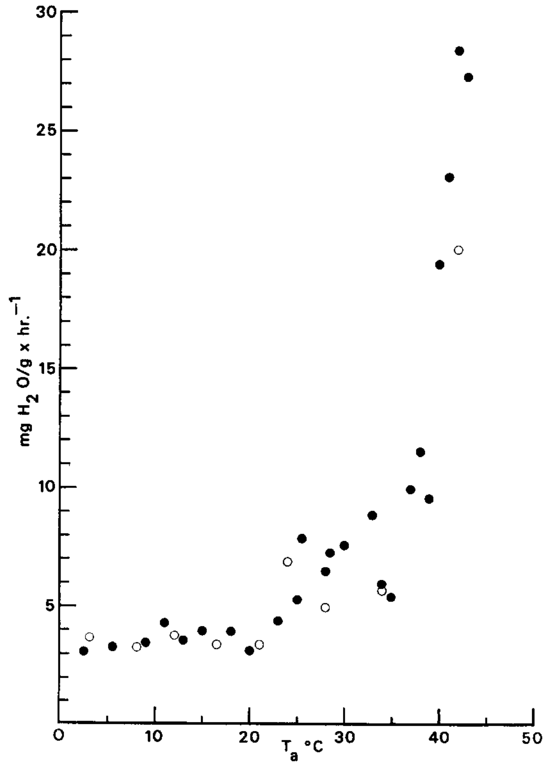

FIGURE 2. Evaporative water loss of 15 Red-breasted Nuthatches in mg($g \times hr)^{-1}$, as a function of ambient temperature (T_a°C). Closed and open circles represent summer and winter birds, respectively.

EVAPORATIVE WATER LOSS

Evaporative water loss increased directly with rising ambient temperature, though not at a constant rate (fig. 2). From 0 to 21°C, water loss was relatively constant and remained below 5 mg($g \times hr)^{-1}$. From 22 to 39°C, water loss increased linearly with increasing temperature ($Q_{10} = 2.2$). Above 39°C, water loss increased abruptly, doubling at 40°C and tripling at 42°C.

CARBON DIOXIDE PRODUCTION

Carbon dioxide production of both winter and summer birds increased as temperature dropped from 30 to -25°C (fig. 3). Below -25°C, carbon dioxide production fell off

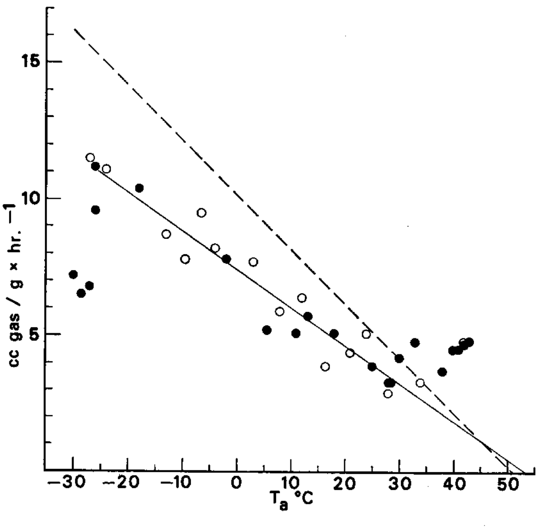

FIGURE 3. Carbon dioxide production of 10 Red-breasted Nuthatches as a function of ambient temperature (T_a°C). Closed and open circles represent summer and winter birds, respectively. The solid line is the linear regression for the combined summer and winter values of carbon dioxide production [cc CO_2 ($g \times hr)^{-1}$] between 30 and -25°C. The dotted line is the linear regression for oxygen consumption [cc O_2 ($g \times hr)^{-1}$] taken from figure 1.

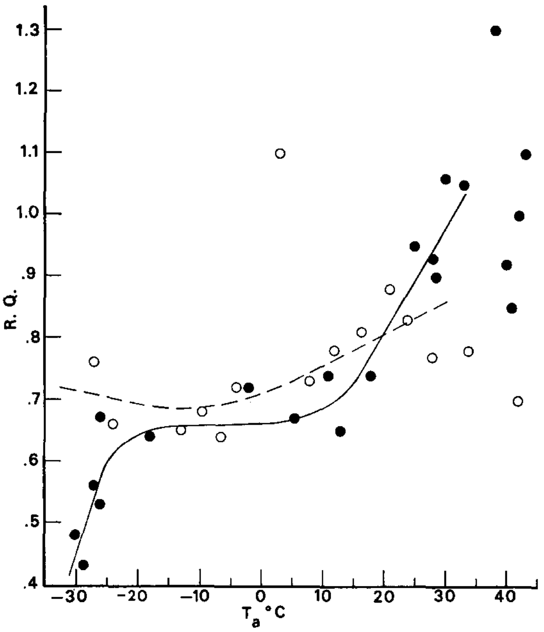

FIGURE 4. Respiratory quotients of 10 Red-breasted Nuthatches as a function of ambient temperature (T_a°C). Closed and open circles represent summer and winter birds, respectively. The solid line (summer birds) and broken line (winter birds) represent the best eye-fitted lines between 30° and −30°C.

sharply only in the summer group. Linear regression lines for carbon dioxide production between 30 and −25°C are: (1) for the summer birds, $y = 7.26 - 0.135x$ (standard error of estimate $= 0.69$, $n = 10$), (2) for the winter birds, $y = 7.45 - 0.143x$ (standard error of estimate $= 0.81$, $n = 12$), and (3) for summer and winter birds combined, $y = 7.39 - 0.140x$ (standard error of estimate $= 0.73$, $n = 22$), where $y = \text{cc } CO_2(g \times hr)^{-1}$, and x = ambient temperature in °C.

Respiratory quotients varying from 0.43 to 1.3 are plotted in relation to ambient temperatures in figure 4. The graph shows a direct correlation between respiratory quotients and temperature. Summer birds displayed the greatest variation, including the extremes at both the upper and lower ends of the temperature scale.

DISCUSSION

OXYGEN CONSUMPTION

The resting metabolic rate in the Red-breasted Nuthatch is similar to the value [3.58 cc $O_2(g \times hr)^{-1}$] predicted by Lasiewski and Dawson (1967) equation for passerines, but is more than 40 per cent greater than the value [2.17 cc $O_2(g \times hr)^{-1}$] predicted by their equation for nonpasserines. Thus, our data support their hypothesis that passerines have a greater metabolic rate than nonpasserines of comparable size.

TABLE 2. Slope values for oxygen consumption in some small birds.

Species	Weight (g)	Slope value cc $O_2(g - hr - °C)^{-1}$
Red-breasted Nuthatch	11.2	0.20
House Wren (calculated by Lasiewski 1963 from Kendeigh 1939)	10.0	0.27
Zebra Finch (Calder 1964)	11.7	0.29
Black-rumped Waxbill (Lasiewski et al. 1964)	6–7	0.40

The values for oxygen consumption obtained from the four winter birds agree with the values obtained from the 15 summer birds (fig. 1). The linear and curvilinear regression lines of summer birds measured below 35°C are statistically similar ($P > 0.05$) to those of winter birds, indicating that the best fit lines and equations should be those utilizing combined data for both summer and winter birds (table 1, fig. 1).

Because neither the summer nor the winter birds were molting, the agreement between summer and winter oxygen consumption values may indicate that the insulative quality of the feathers remained constant. The slope of linear regression for oxygen consumption in the Red-breasted Nuthatch is less steep than comparable linear slopes for the Zebra Finch, Black-rumped Waxbill, or House Wren (table 2). These slope values represent thermal conductance, and indicate that the nuthatch possesses a more effective insulation than these other small birds, which are resident in or migrate to warm climates. Since metabolic rates in Hoary and Common Redpolls were determined from food consumption studies conducted over several days (Brooks 1968), they are not directly comparable to those of the nuthatch. Brooks' results indicate, however, that these arctic passerines probably possess a plumage with greater insulative value than non-arctic passerines. By maintaining these redpolls at a series of constant temperatures he found their lower and upper limits of temperature tolerance (those temperatures at which half the birds die) to be −34 to 38°C or higher for the Hoary Redpoll, and −27 to 38°C for the Common Redpoll. These values are lower than for any other passerine similarly studied. He also notes that these birds possess down feathers in their apteryia, and, when subjected to high temperatures, they reduced their insulative covering by plucking these as well as their contour feathers.

The curvilinear and linear regression lines representing increased oxygen consumption below 35°C (fig. 1) extrapolate to zero metabolism at 58 and 51°C, respectively, values which are far above the range of normal body temperatures for this nuthatch (42–43°C, Wetmore 1921). Resting metabolic rate, represented by the horizontal line in figure 1, crosses these regression lines between 33 and 34°C. A regression line for increased oxygen consumption, fitted by eye to extrapolate to zero metabolism at 42°C, crosses the horizontal line at 26°C (fig. 1). The differences in slope and lower critical temperature for the calculated and the eye-fitted regressions all suggest non-conformance to Newton's law of cooling for this species, with no well defined lower critical temperature and a gradual, rather than an abrupt, transition from physical to chemical thermoregulation. This relationship indicates that thermal conductance may have decreased over a wide range of temperatures. This may have resulted from a slight hypothermic response by these birds at lower temperatures (Scholander et al. 1950). Although body temperatures were not measured in this study, slight hypothermia in response to lower temperatures has been reported regularly for other birds (Dawson 1958; Steen 1958; Misch 1960; Hart 1962; West 1962; King 1964; Lasiewski and Dawson 1964; Greenwald et al. 1967).

The increase in oxygen consumption at ambient temperatures above 39°C reflects the energy expended in evaporative cooling. The birds were often observed in the summer (during captivity and in the wild) hanging upside down with feathers tightly compressed, mouths agape and panting.

During the day, the nuthatch obviously produces heat by activity, but during cold nights it, like other birds, probably shivers to produce the required body heat (Steen and Enger 1957; Hart 1962; West 1965). Shivering movements were observed in nuthatches on the perch of the animal chamber immediately following exposure to cold.

Moore (1945) discussed the possibility that birds could conserve heat by roosting in cavities and other sheltered spots during the winter night. Kendeigh (1961) showed that the House Sparrow, *Passer domesticus*, conserved energy roosting in a nest box, and suggested that such behavior may be the factor allowing northward extension of many small species. Roosting habits of the Red-breasted Nuthatch are undescribed, but we found them utilizing nest boxes in the outdoor flight cage on two cold, windy winter nights. At other times the birds roosted in the sheltered corners of the cage. In the congeneric Pigmy Nuthatch (*Sitta pygmaea*) and the Brown-headed Nuthatch (*S. pusilla*), communal roosting in cavities is common (Knorr 1957; Norris 1958).

EVAPORATIVE WATER LOSS AND DISSIPATION OF METABOLIC HEAT

In an open flow system the relative humidity in the animal chamber is inversely related to the rate of air flow through it (Lasiewski et al. 1966). The relative humidity, in turn, determines the amount of water that can be evaporated from the respiratory surface (King and Farner 1964). From the formula

$$\%RH = 100\,\frac{x/y}{z}$$

where x is the amount of water vapor added in mg/min, y is the air flow per minute, and z is the density of saturated steam at the temperature of the chamber, it was calculated that in these experiments the relative humidity of the chamber was never over 15 per cent.

Respiratory water loss from nuthatches at ambient temperatures below 39°C represents their obligatory water loss (fig. 2). The gradual rise in water loss between 22 and 39°C reflects the ability of warmer air to carry more water rather than any active efforts of the birds to lose heat. At ambient temperatures near 25°C, obligatory water loss represents about 19 per cent of the body weight per day. Thus even at moderate temperatures the Red-breasted Nuthatch is faced with a water loss problem of about the same magnitude as that of the Zebra Finch, but less than that of the Black-rumped Waxbill (21 and 31 per cent body weight per day, respectively, Bartholomew and Cade 1963). In the summer, however, when water loss could be a problem, the nuthatch, unlike these granivorous species, eats mainly insects, which provide a more succulent diet.

The values for water loss and oxygen consumption both slope sharply upward at approximately 40°C (figs. 1, 2), indicating that panting is then initiated to augment heat loss.

Oxygen consumption and respiratory water loss were measured simultaneously, enabling us to estimate the relative effectiveness of evaporative cooling. This relationship is

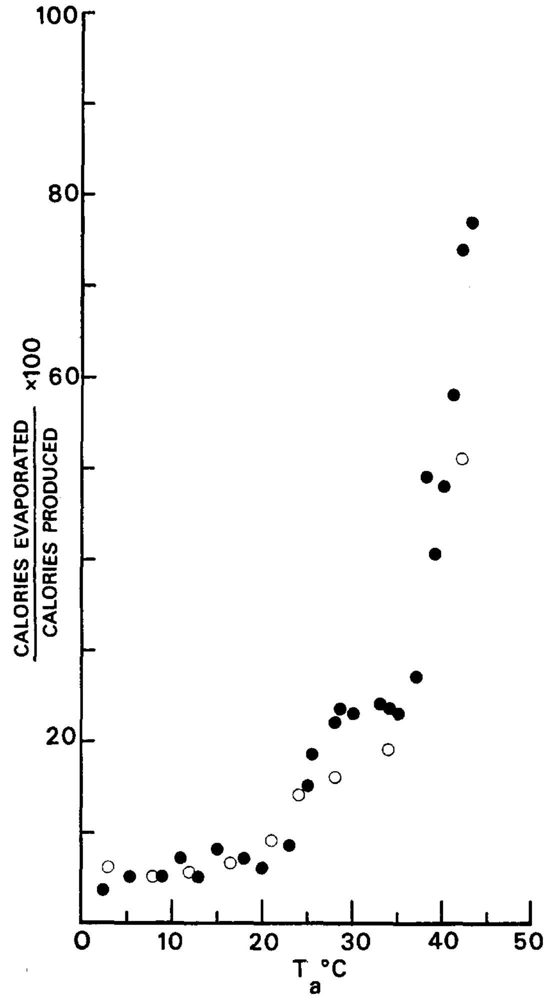

FIGURE 5. The ratio of calories evaporated to calories produced (e/p ratio) for 15 Red-breasted Nuthatches as a function of ambient temperature (T_a°C). Closed and open circles represent summer and winter birds, respectively.

shown in figure 5 as the e/p ratio (e = the heat loss through evaporation; p = the metabolic heat produced), which illustrates the per cent of metabolic heat lost by evaporative cooling. The relative humidity in the animal chamber was low during these experiments, and the nuthatches utilized evaporative cooling quite effectively. At the highest ambient temperatures (42 and 43°C) the nuthatches dissipated 74–77 per cent of their metabolic heat. King and Farner (1964) stated that birds, by tolerating limited hyperthermia at high ambient temperatures, increase passive heat loss to the environment, thus reducing the loss of valuable water via evaporative cooling. Since our ambient temperatures never exceeded Wetmore's (1921) reported body temperature of these nuthatches, evaporative cooling would not have had to account for 100 per cent of the heat dissipated. The birds may have remained in heat balance by undergoing slight hyperthermia.

CARBON DIOXIDE PRODUCTION AND RESPIRATORY QUOTIENTS

Summer regressions for the increasing carbon dioxide production between 30 and -25°C did not differ significantly from those for winter birds ($P > 0.05$). The equation combining the summer and winter values, therefore, was taken to be the best expression of the increased carbon dioxide production.

The regression lines for increased carbon dioxide production and oxygen consumption diverge as temperature decreases (fig. 3). Because of this divergence, respiratory quotients calculated directly from the respective points on the two lines slowly rise with temperature from 0.73 at -35°, to 0.79 at 40°C. However, when each individual respiratory quotient was plotted against temperature (fig. 4), this effect was not seen. Instead, summer respiratory quotients declined sharply between 30 and 15°C, while winter values declined more gradually between 30 and -5°C (fig. 4).

Below -25°C, values for both carbon dioxide production and respiratory quotient in the summer group fell below those for the winter group. These differences in respiratory quotient and in carbon dioxide production below -25°C suggest a seasonal difference in intermediary metabolism which is not observable from the data for oxygen consumption.

Several authors (Kendeigh 1944; Salt 1952; Wallgren 1954) have found that small passerines reach a postabsorptive condition characterized by respiratory quotients of 0.70–0.75 following a fast of 2–3 hr. Exceptions to this have been reported for the Red and White-winged Crossbills, *Loxia curvirostra* and *L. leucoptera* (Dawson and Tordoff 1964), which possess well developed crops and are able to store relatively large amounts of food for long periods. Our autopsy of one nuthatch revealed no apparent crop.

Several respiratory quotients of nuthatches were taken at temperatures within or near the zone of thermoneutrality (31–38°C). Two summer birds previously exposed to temperatures at least 10 degrees colder for 3–5 hr gave respiratory quotients of 1.05 and 1.30. Another summer bird previously exposed to room temperature had hourly respiratory quotients of 1.00, 1.00, 1.20, 1.20, and 1.00. One winter bird previously exposed for 5 hr to a temperature 20 degrees colder had a respiratory quotient of 0.78. Another bird tested during the winter at 34°C, with a previous exposure to room temperature, gave respiratory quotients of 0.73 and 0.78 after 2 and 6 hr, respectively. Winter nuthatches, therefore, appear to reach postabsorptive respiratory quotients faster than do summer birds, which may also suggest a seasonal metabolic difference.

At temperatures above 40°C all birds panted intermittently or continuously. Such irregularity in respiratory activity might cause variability in respiratory quotients (i.e., panting could elevate respiratory quotients by excessive "blow off" of blood carbon dioxide from the lungs). However, the postabsorptive respiratory quotient (0.70) of the winter bird tested supports the suggestion that winter birds reach post absorptive values faster than do summer birds, which had respiratory quotients ranging from 0.85 to 1.10 (fig. 4).

Red-breasted Nuthatches exposed to ambient temperatures below 20°C showed respiratory quotients below 0.80 even after fasting no more than 1 hr. Thus, absorptive birds may have low respiratory quotients when exposed to short term cold stress. The occurrence of postabsorptive respiratory quotients in absorptive animals as a response to short term cold stress has also been demonstrated in rats (Page and Chenier 1953; Page 1957).

Respiratory quotients below 0.70 may indicate an incomplete oxidation of fat and interconversions among fat, protein, and carbohydrates (King 1957), or the synthesis of carbohydrates from fats (Henry et al. 1934; Kleiber 1961), whereas respiratory quotients above 1.0 indicate the synthesis of fat from carbohydrates (Kleiber 1961). It has been pointed out, however, that short term respiratory quotients alone may not be valid expressions of intermediary metabolism (Kleiber 1961; Masoro 1966). Until these views are clarified we are reluctant to interpret further the variable responses of our short term respiratory quotients to temperature.

SUMMARY

Oxygen consumption, evaporative water loss, and carbon dioxide production were measured in both summer and winter Red-breasted Nuthatches over an ambient temperature range of 73°C (–30 to 43°C) to determine possible seasonal changes. Oxygen consumption did not differ significantly between summer and winter birds. The average increase in oxygen consumption measured at temperatures below 35°C is expressed as linear and curvilinear regression equations of $y = 10.20 - 0.20x$, and $y = 9.92 + 0.00074x^2 - 0.21x$, respectively. For birds measured within the poorly defined thermoneutral zone (33–38°C) mean oxygen consumption was 3.71 cc $O_2(g \times hr)^{-1}$, which agrees with the predicted value for passerines.

At ambient temperatures near its normal body temperature, the nuthatch can dissipate more than 70 per cent of its metabolic heat by panting. Its obligatory water loss of 19 per cent of its body weight per day at 25°C suggests that it might face serious problems with water loss at high temperatures or during stressful conditions.

Carbon dioxide production decreased as temperature increased between –25 and 30°C, but summer values did not differ significantly from winter values and yielded the equation $y = 7.39 - 0.140x$. Below –25°C, carbon dioxide production dropped markedly in summer birds but not in the winter birds. Respiratory quotients increased more rapidly with temperature (–30 to 30°C) in summer birds, suggesting a seasonal metabolic difference in response to short term temperature changes.

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