SEASONAL VARIATION IN THE METABOLISM AND THYROID ACTIVITY OF THE BLACK-CAPPED CHICKADEE (*PARUS ATRICAPILLUS*)

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Few problems are so fundamental to ecological and systematic studies as those of how organisms adapt to live in their environments. The direct measurement of oxygen consumption as an indicator of metabolic activity is a technique widely used to elucidate some of these adaptations. Such studies of homeotherms have shown, for the most part, that measured differences in standard metabolism can be accounted for by differences in size among species (Brody and Proctor 1932) although King and Farner (1961) and Lasiewski and Dawson (1967) have identified both body size and taxonomic deviations from this generalization. This suggests that the thermoregulatory adaptive differences among populations of homeotherms that allow them to inhabit the climatically diverse regions of the earth must involve modifications of the insulative coat and behavioral responses rather than major metabolic adjustments. A number of recent investigators (Bartholomew et al. 1962; Bartholomew and MacMillen 1961; Dawson and Bennett 1973; Hudson 1965; Hudson and Kimzey 1966; Hudson and Rummel 1966; McNab and Morrison 1963; Rising 1969) have described several species of birds and mammals with basal metabolic rates lower than those that would have been predicted on the basis of body size. With few exceptions, these studies have not been concerned with whether homeotherms show seasonal variations in basal metabolism, variations which may allow birds and mammals to live in an environment that features significant seasonal temperature variation.

Heat loss is always greatest when ambient temperatures are lowest, and thus mechanisms serving to compensate for such loss, or to retard it, should be most effective during the winter. The ability of adult birds to maintain constant body temperatures at low temperatures has generally been considered entirely explicable in terms of an enhanced metabolism produced by shivering thermogenesis and a

decrease in heat loss due to insulative adjustments (Hart 1958; Steen and Enger 1957; West 1965). Nonshivering thermogenesis is recognized as playing an important role in thermoregulation by many small mammals (Davis and Mayer 1955; Depocas et al. 1957; Hart 1958; West 1965). Chaffee and Mayhew (1964) and Wekstein and Zolman (1968) suggest that nonshivering thermogenesis occurs in House Sparrows (*Passer domesticus*) and newly hatched Domestic Chickens (*Gallus gallus*). El Halawani et al. (1970) observed nonshivering thermogenesis in adult chickens acclimated to ambient temperatures of 5°C for periods of 5 and 9 months. Even though norepinephrine is generally considered to be the principal agent responsible for nonshivering thermogenesis, the calorigenic effect of thyroid hormones is also considered of great significance for the induction of nonshivering thermogenesis (Jansky 1973). Increased levels of thyroxine, which accentuate the calorigenic effect of norepinephrine, are found in mammals acclimated to low temperatures (Hart 1958). Freeman (1970) attributed nonshivering thermogenesis in chickens to the calorigenic effect of thyroid hormones. In view of the increased evidence that nonshivering thermogenesis in birds may be an important mechanism for adapting to low temperatures, it is possible that seasonal changes in thyroid secretion may accompany seasonal adjustments in metabolism and insulation (Dawson 1958; Hart 1962; West and Hart 1966) as important means for coping with different temperature regimens.

To ascertain whether there is seasonal variation in (1) standard metabolism, (2) metabolism at low ambient temperatures, and (3) thyroid activity, we studied Black-capped Chickadees (*Parus atricapillus*) taken from the field in both summer and winter. Chickadees inhabit northern temperate regions and are resident (at least to the extent that some individuals are present throughout their range at all seasons), and thus are annually exposed to considerable temperature extremes. Their

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small size (ca. 10 g) and arboreal habits result in the concomitant problems of (1) an unfavorable surface-volume ratio and (2) intimate exposure to the most severe ambient conditions. Additional data are needed since there have been relatively few studies of the bioenergetic problems confronting small passerines in cold climates (Hissa and Palokangas 1970; Lasiewski et al. 1964; Muggas and Templeton 1970; West 1972).

MATERIALS AND METHODS

Chickadees were captured with mist nets set at various localities in the vicinity of Ithaca, Tompkins County, New York. The winter birds were taken in the last 2 weeks of February 1969 (19–27 February), and were subjected to tests throughout March to mid-April; summer birds were taken from late July through mid-August 1969 (27 July to 14 August) and were tested through August. Although some movement of winter populations occurs in Black-capped Chickadees in the northeast, including New York (Odum 1942), we believe that the birds used in the present study were year-round residents of the Ithaca region, since some of the birds captured and marked in the autumn were recaptured during the winter. One adult bird studied in the summer had been banded at the locality of capture on 11 April 1969. In a study of chickadee movement in the Ithaca area carried out during the winter of 1968–69, very little immigration (less than 10%) occurred, and fewer than 10% emigrated (or wandered) more than 1.5 miles from the feeding site at which they were banded in early winter (E. Mueller, pers. comm.). Many of the individuals used in the summer tests were perhaps only 3 or 4 months old. Chickadees less than approximately 8 months old can be differentiated from older birds by the extent of skull ossification. Some of the summer birds were less than 8 months old and therefore must have hatched in the previous spring. No differences in metabolic responses between younger and older chickadees were detected.

Chickadees are not conspicuously sexually dimorphic, although males average somewhat larger than females (Brewer 1963; Rising 1968). Thus, it was impossible to determine the sexes of individuals in advance of the testing. However, birds were autopsied when they died and no conspicuous differences in the physiological parameters could be correlated with sex differences.

The winter birds were kept in two different cages, one indoors and one outdoors. Both cages were approximately cubical, were about 600 ft³ in volume, and had abundant perches. Nest boxes were occasionally used for roosting (but only by a few of the outdoor birds on the coldest nights). There was no tendency for communal roosting. Food and water were supplied ad libitum. Snow was supplied as water for the outdoor birds when temperatures were below freezing, and all birds were given sunflower seeds, raw peanuts, beef suet, and occasionally mealworm larvae. Since the outdoor cage was partially open, natural photoperiods and nearly natural temperatures prevailed. Natural photoperiods were simulated in the indoor cage by means of two sets of lights controlled by time clocks. One time clock was connected with a 15-watt bulb to provide 0.5 hr dawn and dusk illumination, whereas the other clock con-

trolled four fluorescent lights in the room. On the basis of readings from maximum-minimum thermometers, ambient temperatures of indoor cages ranged from 28–33°C. In the outdoor cage, the ambient temperature ranged between –20 and +15°C in the winter and +4 to +30°C in the summer.

Oxygen consumption was measured with an open flow system, using a Beckman G-2 paramagnetic oxygen analyzer. A 1-pint paint can with a double lip seal was used as a metabolism chamber. The birds, tested singly, sat on a ¼ × ¼ inch mesh hardware cloth platform elevated above the floor of the can which was covered with approximately ¼-inch layer of mineral oil to prevent excreted water from mixing with evaporated water. The airflow through the chamber was 750 ml/min. This flow rate was sufficient to allow efficient evaporative cooling at the higher ambient temperatures according to the formula of Lasiewski et al. (1966). The air entering and leaving the chamber was dried in tubes containing $CaSO_4$ (indicating Drierite). The CO_2 from the bird was absorbed by Ascarite prior to the entry of air into the oxygen analyzer. The amount of water lost by the birds was determined by weighing the desiccating tubes, and the oxygen consumption was calculated after the method of Depocas and Hart (1957), using their upstream formula and the airflow corrected to STP. All birds were tested at night, at least 3 hr after dusk, at which time they were assumed to be postabsorptive. The birds were retained in the chamber for a variable amount of time, ranging from 2.5 to 12 hr, at least until the oxygen consumption was stable and minimal. The drying tubes used to measure evaporative water loss were attached after the oxygen consumption had stabilized. Body temperatures of the summer birds were measured by pressing the end of a small animal thermistor firmly under the wing in the unfeathered axillary area. Body temperatures were measured to nearest 0.5°C, but would only approximate core temperatures. Birds were weighed both before and after experimental runs, and the final weight for a given night was used to calculate the oxygen consumption per gram of body weight. The ambient temperature was determined from a copper-constantan thermocouple in the metabolism chamber connected to a Leeds and Northrup Speedomax G recording potentiometer.

To measure thyroid activity, 0.5 ml of normal physiological saline containing 5 µc of ^{125}I was injected into the pectoralis muscle of birds from all experimental groups. The indoor birds were allowed one week to adjust to the new temperature regimen prior to injection. This amount of radioisotope is far less than would damage the thyroid gland (Bailey 1953). To measure the amount of radioactive iodine in the thyroid glands, the furcular region of the bird was pressed gently over the surface crystal of a scintillation counter covered with a Lucite plate above a lead shield 75 mm in diameter and 55 mm thick, containing a hole 10 mm in diameter to collimate the emitted radioactivity. The detector was connected to a Nuclear Chicago 1085 Auto-Gamma scaler with a dual scaler/timer and printing lister. The bird was repeatedly repositioned on the Lucite plate over to the orifice in the lead collimator until the maximum count was obtained. Remarkably close replicate counts were obtained for any one individual, though the maximum neck counts varied among individuals (from ca. 9000–14,000 counts/min), doubtless reflecting in part variation in the amount of ^{125}I assimilated by the birds. Neck counts were first made 24 hr following
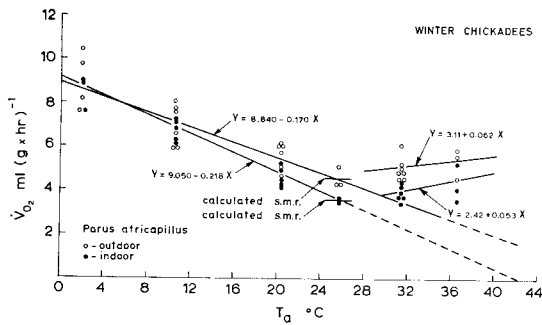
FIGURE 1. The oxygen consumption of Black-capped Chickadees (*Parus atricapillus*) from Ithaca, New York, at six test temperatures. Seven birds (open circles) were kept in an outdoor cage, and five birds (closed circles) were kept in an indoor cage. Not every bird was tested at each temperature. The upper regression line is for outdoor birds, the lower line for indoor birds. The solid lines are least square fits of the summer and winter values both below and above the thermal neutral zone (calculated SMR). Weights ranged from 9.0 to 12.4 g (av. = 10.3).
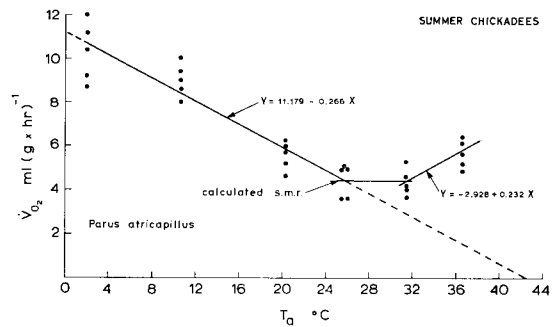
FIGURE 2. The oxygen consumption of eight Black-capped Chickadees captured and tested during the summer. Not every bird was tested at each temperature. The line connecting the points above and below the thermal neutral zone has been fitted by least squares.

injection and periodically thereafter. The rate of uptake and release of the labeled iodine from the gland was expressed as a per cent of the maximum count corrected for the natural decay of the isotope. To adjust means to compensate for loss of individual birds which may have markedly higher or lower counts than the rest of the sample group, the following procedure was used: The neck count of the $n-1$ population before a death was multiplied by the ratio of the count of the surviving population and any succeeding count after the first death. If a second death occurred, this procedure was repeated using a new ratio consisting of the counts of $n-2$ before the second death and any succeeding count multiplied by count prior to the second death.

RESULTS

Analysis of variance (Sokal and Rohlf 1969) for the data on oxygen consumption reveals highly significant ($P < 0.001$) differences in standard metabolism between summer and winter birds and between indoor and outdoor birds. The minimal oxygen consumption of both indoor and outdoor winter chickadees occurred at an ambient temperature of 25.5°C (fig. 1). The standard metabolic rate of the outdoor winter birds was 4.4 cm³ O_2 · (g-hr)$^{-1}$ which is approximately 10–13% greater than values of 3.9–4.0 cm³ O_2 · (g-hr)$^{-1}$ that would be predicted on the basis of body size according to the equation of Lasiewski and Dawson (1967). The standard metabolism of the indoor winter birds was 3.6 cm³ O_2 · (g-hr)$^{-1}$ and is 8–10% lower than predicted. The summer chickadees were measured at two ambient temperatures within the thermal neutral zone and their oxygen consumption was 4.4 cm³ O_2 · (g-hr)$^{-1}$ at both 25.5 and 31.5°C (fig. 2). Their standard metabolism is the same as that measured for the outdoor winter birds.

All of the experimental groups exhibited an elevation in metabolism at the highest T_a to which they were exposed, viz., 36.5°C. This elevation was more pronounced among the outdoor winter and summer birds than among the indoor winter birds. Both groups of winter birds have statistically similar ($P > 0.10$) increases in oxygen consumption (fig. 1) at ambient temperatures below thermal neutrality. The slope of a regression line drawn by eye through the data from 2 to 25°C for the outdoor winter birds is –0.170 cm³ O_2 · (g-hr °C)$^{-1}$ and the Y-intercept is 8.84. The slope of the regression line between 2.0 and 25.2°C for the indoor bird is –0.218 cm³ O_2 · (g-hr °C)$^{-1}$ and the Y-intercept is 9.05. The metabolism of the summer birds increased more with decreasing ambient temperatures than did either of the winter groups (figs. 1 and 2). The regression line between 2 and 25°C for summer birds is –0.266 cm³ O_2 · (g-hr°C)$^{-1}$ and the Y-intercept is 11.18. The slope of this line may be significantly greater than that for the outdoor winter birds ($P < 0.10$), but is not significantly greater than that for the indoor winter birds ($P > 0.10$).

Chickadees may lose up to 400 mg of water/hr by evaporation at the higher ambient temperatures. Losses of less than 100 mg/hr were usual for ambient temperatures below 31.5°C. The percentage of the metabolic heat that could be dissipated by evaporative cooling, assuming that 4.8 cal of heat are produced for each milliliter of O_2 consumed and 0.58 cal dissipated for each milliliter of water lost by evaporation, varied considerably. The chickadees did not dissipate all of their metabolic heat by evaporative cooling at the highest ambient temperature to which they were exposed. They dissipated a maximum of 72.2% at 36.5°C and 59.3% at 31.5°C.
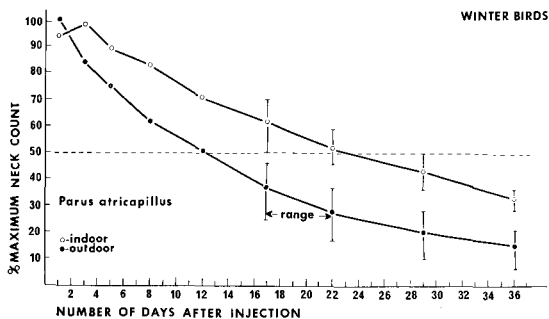
FIGURE 3. The release of ^{125}I from thyroid glands of Black-capped Chickadees kept in an outdoor cage during the winter (closed circles) and those kept in an indoor cage (open circles) at the same season. There were four birds in each group. Ranges are indicated by the vertical lines.
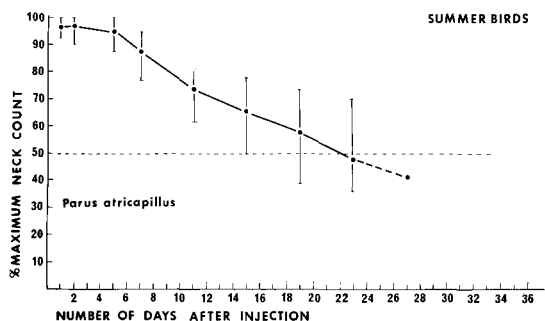
FIGURE 4. The release of ^{125}I from thyroid glands of Black-capped Chickadees during the summer. Ranges are indicated by the vertical lines. Eight birds were measured on days 1, 3, and 5; six on days 7, 11, and 15; and five on days 19 and 23. (See text for procedure of adjusting means.)

The few data on body temperatures (T_b) we were able to obtain from quiescent birds at different ambient temperatures (T_a), all of which were from the summer birds, indicate considerable lability in T_b. The body temperature varied 4.5°C at ambient temperatures between 10.5 and 36.5°C. In general, the higher T_b's were characteristic of birds exposed to the highest T_a's, whereas the lowest T_b's were from birds at the lowest T_a's.

The outdoor winter birds exhibited a faster rate of ^{125}I uptake than the other groups [the maximal neck counts of radioactive iodine occurred within 24 hr after injection, whereas maximum neck counts for the indoor winter birds and the summer birds were attained between the 1st and 5th days after injection (figs. 3 and 4)]. The biological half-life of thyroidal ^{125}I was about 12 days in winter outdoor birds, 24 days for the winter indoor birds, and 22.5 days for summer birds.

DISCUSSION

Both the standard metabolic rate (SMR) and thyroid activity of Black-capped Chickadees from the Ithaca area vary seasonally. The apparent depression of the SMR of the indoor winter chickadees is similar in magnitude to that found in some populations of House Sparrows (Hudson and Kimzey 1966) and orioles (*Icterus galbula, I. bullockii*) (Rising 1969) that live in warm climates. The advantage conferred by a lower SMR may be the reduction of the number of calories that would need to be dissipated by evaporation of water in order to maintain homeothermy, permitting activity at higher ambient temperatures or more intense activity at high ambient temperatures. Conservation of water may be more significant to chickadees, inhabitants of mesic woodlands, than one might think. A 10 g

chickadee with an oxygen consumption of 5.0 cm^3 O_2 · $(g\text{-}hr)^{-1}$ produces 240 calories in 1 hr. To dissipate all of this heat by evaporative cooling would require the dissipation of slightly more than 400 mg of water/hr, or approximately 4% of the bird's body weight. And these calculations do not take into consideration the increment of heat to be dissipated due to flight. It is obvious that a chickadee could not sustain such a loss of body water for long without replenishment. Mechanisms that allow for a slight reduction in the resting metabolism and hence the heat production may be clearly adaptive when viewed in their ecological context.

The conspicuous differences in the rates of both uptake and release of radioiodine by the thyroid glands of the chickadee during different seasons and under different temperature regimens can be interpreted to indicate different levels of thyroid activity (Tepperman 1962). Presumably, a rapid uptake and release of radioiodine signify rapid synthesis and release of thyroxine and vice versa. It is thought that both thyroxine and triiodothyronine uncouple electron transfer, permitting oxidative processes to continue but redirecting chemical energy from phosphorylation of ADP to the production of heat (Turner 1966). Thus, the greater thyroid activity of the outdoor winter birds, as evidenced by the rapid secretion of radioiodine, could well contribute to greater basal heat production than was observed in indoor birds. On the other hand, the most significant change may be a reduction of thyroid activity, as observed in birds exposed to warmer environments. Chaffee et al. (1963) found no increase in liver succinoxidase—an indicator of general cellular oxidative activity—in cold-acclimated House Sparrows such as occurs in cold-acclimated small ro-

dents. Yet Chaffee and Mayhew (1964) found
a striking decrease in liver succinoxidase ac-
tivity in heat-acclimated House Sparrows.
They suggest that the central location of the
liver would retard the dissipation of heat from
that organ so that suppression of thermogenesis
in the liver could be of considerable adaptive
value to birds faced with the necessity of
heat dissipation. Thus, thyroid performance
of the chickadee may be interpreted as a sup-
pression of activity in the summer rather than
enhancement during the winter.

Presumably, the two winter experimental
groups of chickadees had similar insulative
coats when captured, whereas the summer
birds probably had a less dense feather coat
when captured. The similarities in the meta-
bolic responses of the two winter experimental
groups at ambient temperatures below thermo-
neutrality indicate similar insulation values,
whereas the consistently higher metabolic rates
of summer birds at the lower ambient tem-
peratures suggest less effective insulation. The
reduced thyroid activity of summer birds and
indoor winter birds could lead to lower heat
production. Because of their reduced insula-
tion, summer birds compensate for their
greater heat loss at all temperatures, including
their thermoneutral temperature, by raising
their oxygen consumption above levels mea-
sured for the indoor winter birds. To do this
in spite of lower thyroid activity would suggest
increased shivering thermogenesis.

Chickadees are capable of tolerating as
much as a 4.5°C fluctuation in body tempera-
ture, which might have been greater had the
birds been exposed to a wider range of am-
bient temperatures than those used in the
present experiments.

From our results and the earlier work of
Hudson and Kimzey (1966), it is clear that
physiological data can be related to geographi-
cal locality and seasonal changes in climate.
Thus, the standard metabolic rate cannot be
taken as an invariable attribute of a species.
Rather, it is one aspect of a population unit
which should be expected to vary with time
and habitat. Almost certainly, the preoccupa-
tion with size as the single most important
factor influencing metabolic rate does not ade-
quately relate the variation of metabolic data
to ecological context. It is likely that selective
pressures must be intense in many instances
to cause departure from normal responses.
We suspect that careful interpopulational and
interseasonal studies of several taxa will show
that metabolic lability is the rule rather than
the exception.

SUMMARY

The standard metabolism of the Black-capped
Chickadee in winter is 4.4 cm³ $O_2 \cdot$ (g-hr)$^{-1}$
for birds maintained under natural conditions
and 3.6 cm³ $O_2 \cdot$ (g-hr)$^{-1}$ for birds kept in the
laboratory, values which are 10% above to
10% below, respectively, those expected on
the basis of body size.

The nocturnal body temperature of chicka-
dees measured during the summer was labile,
ranging from 36 to 40.5°C.

The biological half-life of radioiodine re-
leased from the thyroid gland was 12 days for
winter outdoor birds and 22.5 days for summer
birds, while the biological half-life of ¹²⁵I
in winter indoor birds was 24 days. These
data are interpreted to indicate a reduction
in thyroid activity with prolonged exposure
to relatively high ambient temperatures.

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