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A COMPARATIVE STUDY ON THE ENERGETICS OF THE
BLACK-CAPPED AND CAROLINA CHICKADEES,
PARUS ATRICAPILLUS AND PARUS CAROLINENSIS

DISSERTATION

Presented in Partial Fulfillment of the Requirements for
the Degree Doctor of Philosophy in the Graduate
School of The Ohio State University

By

John Stephen Munzinger, A.B., M.S.

******

The Ohio State University
1974

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INTRODUCTION

Comparative studies on taxonomic units have produced important information on members of those units, providing bases on which the members may be related to or distinguished from one another. Evolutionary patterns, species differences, population distribution, and geographical variation have been some of the results of such studies. Such has been true in the case of the genus *Parus*, which is divided into two subgenera, *Poecile* (the chickadees) and *Baeolophus* (the crested tits). The chickadees distinguish themselves by possessing either black caps or brown caps and are generally considered as allopatric in North America (Dixon, 1961), although one brown-capped species (*Parus hudsonicus*) does overlap geographically with one black-capped species (*P. atricapillus*). Of all the parids, two black-capped species, the Black-capped Chickadee (*P. atricapillus*) and the Carolina Chickadee (*P. carolinensis*), are considered to be the most similar. The two species are small, woodland passerines (Paridae), which occur in temperate North America. Both are strikingly similar in aspects of morphology, biology, and ecology which can be appreciated by studying the works of Odum (1941a, b; 1942)
and Brewer (1961, 1963). If one omits the references to the geographical occurrence of the Black-capped Chickadee in Odum's work and simply refers to the bird as "chickadee", the difficulty in interpreting which species life history Odum is describing is apparent. Brewer explicitly describes the similarity of the two species, comparing the behavior and interrelationships of them.

Although the Black-capped and Carolina Chickadees are similar or identical in aspects of size, weight, plumage, life history, and voice (Brewer, 1963), they differ in geographical range. The Black-capped Chickadee has the largest range of all North American chickadees, extending over the entire northern United States, through southern and middle Canada to southern Alaska. The Carolina Chickadee replaces the Black-capped Chickadee in the southern and mid-eastern United States. In Missouri and Illinois, the boundary of the two chickadees is contiguous and Brewer (1961, 1963) records that hybridization occurs. East of this region, the northern boundary of the Carolina and the southern boundary of the Black-capped are poorly known, although a gap of several miles exists between the range limits. Brewer (1963) cites evidence of the variance of this hiatus from year to year, as well as from region to region. Because of this hiatus, which is sometimes referred to as a zone of range overlap, the exact delimitation of ranges in Ohio has been a subject of discussion. This is
true especially because of the migratory nature of the Black-capped, which sometimes appears to "invade" Ohio (Hicks, 1935; Thomas, 1958). Generally, the Black-capped is described as a species wintering in northern Ohio, frequently extending south to the Columbus area. The bird is considered a resident or breeding species of the extreme northern portions of the state (Thomas, 1958), especially in the northeastern counties (Trautman, personal communication). The Carolina is regarded as a resident species and Thomas (1958) describes it as occupying "roughly the southern two-thirds of Ohio, being more common toward the southern portions of the state."

In addition to the hybrid populations of Missouri and Illinois (Brewer, 1963), Rising (1968) has studied hybridization in Kansas where the two species are in contact. The only other evidence of hybridization is that presented by Tanner (1952) and Johnston (1971), which is the result of disjunct populations of Black-capped Chickadees in the southern Appalachians. Hybridization does not seem to be widespread, and the studies cited above show that it occurs in those areas where geographical boundaries are contiguous between the two species.

For the Black-capped Chickadee and Carolina Chickadee to remain isolated, however similar they may be, specific reproductive and ecological isolating mechanisms must exist. That this is true is indicated in the literature on these
two species. Considering the geographical range of each, the Black-capped extending north to central or southern Alaska and the Carolina as far south as the Gulf Coast (Reilly, 1968), one wonders if other aspects, such as physiological factors, might also provide some limits to the extent to which each species may range. Functionally, organisms are indivisible units and therefore each deals with its environment as a whole (Bartholomew, 1968). Since a group of individual organisms comprise a species, strictly-speaking one could expect each species to deal with its environment individually. Dawson (1954) found physiological differences in examining the energetics of two congeneric species of birds living in close proximity but in slightly different habitats. Considering the fundamental similarities of the Black-capped Chickadee and the Carolina Chickadee but also the difference in range, and therefore the climatic extremes to which each is exposed, one reason for undertaking this study was to determine if there is a difference in the energetics of the two parids. As is true for many families of small-size passerines, little information is available on the physiology of members of those families. Aspects of life history, morphology, and reproductive behavior of chickadees have been extensively studied. Studies on geographical variation and habitat and ecological relationships of parids have also
been extensive (Snow, 1954a, b; Dixon, 1961; Lack, 1971).
The only reference found relating to the physiology of energetics of chickadees was an abstract of a presentation made by Budd (1972). Personal communication with Budd (1974) has helped to confirm this.

A second reason for the study was established as a result of the first. If no difference in energetics is found, could the Black-capped Chickadee and Carolina Chickadee really be two different species? Assuming there is no difference, perhaps *P. atricapillus* and *P. carolinensis* are populations of the same species which distinguish themselves mostly by song and behavior. Brewer (1963) hypothetically reconstructs occurrences in the evolution of the two species from portions of a common stock and argues for a relatively recent divergence. He bases this on the species' extreme similarity in morphology, behavior, and ecology. The present work examines an aspect of the two species which has not been studied before. It is a comparative study of the energetics of two closely related avian species, which occur in similar, temperate woodland habitats. Dawson's studies (1954) involved the energetics of the Brown and Abert Towhees (*Pipilo fuscus* and *P. aberti*); Salt (1952) has examined metabolic responses of three species of finches (*Carpodacus*). The works of Dawson and Salt concern desert fringillids found within each other's ranges but occurring
in dissimilar habitats. Conversely, the present study involves two closely-related small passerines, which occupy similar habitats but generally replace each other geographically (Snow, 1954b).
METHODS AND MATERIALS

Study and Collection Sites

The field and laboratory investigation of this problem extended over a two year period and was performed mostly between the months of October and April. During these months the chickadees could be easily captured because of their tendency to flock in or near feeding areas. Reproductive stress and activities were also minimal at this time of the year. A total of 55 Black-capped Chickadees and 52 Carolina Chickadees was used in determining energetics. In many cases an individual was used in more than one study (Table 1).

Field investigation and collection sites were located in several areas in Ohio. Initially birds were collected only from rural areas of Delaware County. The main area, which extends through the property of six landowners, lies approximately 12 miles north of the city limits of Columbus, is bounded by U. S. Route 23 and Home Road at its southwest corner, and has an area of approximately one-half square mile. A second area was located 10 miles west of the main site and consists of five acres of land along the Scioto River. The habitat of these sites consists of open fields,
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farmland, and wooded areas. Birds taken from these sites were all Carolina Chickadees, although Trautman (personal communication) advised that both species might be encountered in Delaware County.

Collection success in Delaware County was determined to be one bird per eight-hour field day. Because of the paucity of specimens available and the absence of Black-capped Chickadees, several other study and collection areas were established in other areas of the state. The Ohio results of the annual Audubon Christmas Bird Counts (Cruickshank, 1970, 1971, 1972) revealed that large numbers of Black-capped Chickadees and Carolina Chickadees are recorded in Ashtabula and Hamilton Counties respectively. Collection sites in Ashtabula County were located in seven different areas within or just outside the city limits of Ashtabula. All sites were near houses where feeding stations were established by individual residents. One collection site was established in Hamilton County. Another site was located in Clermont County at the Cincinnati Nature Center where several feeding stations were in operation. The habitat there consists of open fields and wooded areas. When a two-day trip was made to either the Ashtabula or Cincinnati area, ten to twelve specimens could be anticipated, which produced a collection rate of five to six specimens per eight-hour field day. In one instance, fourteen Carolinas were captured within a two-hour period.
using both nets and traps.

Identification of all specimens was based on Trautman (1966), size and weight of the bird, and the locale in which each bird was collected. In addition, Trautman (personal communication, 1971-1974) periodically examined live specimens and specimens which had died in captivity to insure that proper identification was being made.

Capture and Maintenance

Feeding stations were used in order to attract chickadees to a study and collection site. These stations consisted either of bird feeders which were established by the local residents of an area or platform-type feeding stations constructed from empty, wooden, wire reels. The reels (approximately 45 cm high with a surface area of 190 cm²) were turned on their sides and raised off the ground using two or three cement blocks. Stations were baited with wild bird seed, peanut butter, and suet over the entire study period except for the late spring and summer months.

Birds were captured by using NEBBA Mist Nets (Bird-Banding, 1969) or treadle-type cage traps (Fig. 1). Totals of 37 and 94 birds were obtained by the two respective methods. Mesh size of the nets was 36 mm. Nets were obtained from E. A. Bergstrom, 37 Old Brooks Road, West Hartford, Conn. (Bird-Banding, 1969). The procedures and
equipment used in netting the birds were similar to those described by Low (Bird-Banding, 1957) and Munzinger (1963). The treadle-type traps (McCamey, 1961), known as McCamey chickadee traps to bird banders, were obtained from D. E. Payne, Route 7, Box 159A, Eugene, Ore. Traps were used at feeding stations and baited with the same type of food present at the station. Excess food at stations was removed or covered (Fig. 2). Sunflower seed proved to be the most successful bait in attracting birds to the collecting areas.

After capture, the birds were transported to The Ohio State University, Columbus, Ohio, where they were weighed and placed in individual cages (28 x 22 x 26 cm). To avoid injury and minimize stress during transportation, birds were placed in pint-size cardboard, ice cream containers, each of which was fitted with a screened air hole and a burlap lining. This was particularly important for those birds being transported from distant areas, viz. Ashtabula, Clermont, and Hamilton Counties. Since these areas necessitated overnight trips, temporary holding facilities had to be established where birds could be housed and fed. Travel to Columbus from distant areas was made during hours of darkness when the birds were naturally more quiescent.

Birds were allowed to adjust to cage and laboratory conditions before experiments were undertaken. They were
Figure 1. Collecting equipment for chickadees, showing disassembled mist net supports, mist net, and McCamey chickadee trap.
Figure 2. McCamey chickadee trap placed over bird feeder at collecting site in Delaware County with Carolina Chickadee.
first housed in a small, quiet greenhouse room for approximately five to seven days, where a natural photoperiod was maintained. Air temperature was maintained at $18 \pm 2^\circ C$. After this period, they were transferred to the physiology laboratory where they were kept in a Sherer-Gillett walk-in environmental room. The room was regulated for a 12-hour photoperiod (0800 - 2000) with a daytime air temperature of $20 \pm 1^\circ C$ and a night-time air temperature of $15 \pm 1^\circ C$. Birds remained here for another five to seven days before experiments commenced.

All chickadees were fed a diet of mixed wild bird seed, supplemented by additional sunflower seeds. Vionate (Squibb), a vitamin supplement, was mixed in peanut butter which was placed in cages about twice a week. At least once a week, this diet was supplemented by meal worm larvae (Tenebrio sp.) or raisins. Water with a small amount of antibiotic (Pura-Mycin by Ralston-Purina) was supplied ad libitum.

Each chickadee was coded with its own number which provided information on the exact location and time of collection. This was also needed to determine which specimens were used in each experiment. Black-capped Chickadees were identified by a red, numbered, plastic band on the right leg; Carolina Chickadees had a yellow band on the left leg.
Field and Laboratory Observations

Throughout the study, observations were made on both species of chickadees in the field, as well as under laboratory conditions. This was done for two basic reasons: (1) To establish guidelines for capturing a sufficient quantity of specimens, and (2) to determine whether any specific behavior patterns could be correlated with specific physiological responses.

One laboratory experiment was run to determine whether chickadees might be induced to use nesting cavities under conditions of decreasing nocturnal ambient temperatures. Sections of old tree stumps with nest holes that had been hollowed out by wrens, woodpeckers, or chickadees were placed in individual cages. Two Black-capped and two Carolina Chickadees were observed over a ten-day period from behind a blind, set up in the environmental walk-in chamber. Observations were made during the last 45 minutes of the photoperiod as the ambient temperature dropped to the nocturnal setting (15°C). Since only one Carolina Chickadee occupied a cavity for one night at 15°C, an effort was made to determine whether a lower ambient temperature would induce the birds to occupy the cavities. The nocturnal setting for the environmental chamber was lowered five degrees every two days until 0°C was reached. Thereafter, the ambient temperature was raised to 10°C for two nights and the experiment was terminated.
Oxygen Consumption (2 Hour)

The standard metabolic rate was studied by measuring the amount of oxygen consumed over a two-hour period of time. Diurnal and nocturnal measurements were made at five degree intervals from $0^\circ$ to $40^\circ$C using a darkened, respiratory chamber. Since standard metabolic rate is based on a postabsorptive state, which is two hours for small passerines (Kendeigh, 1944; Salt, 1952), birds were fasted for at least two hours prior to experimentation.

The oxygen consumed was measured with an open-circuit system connected to a Beckman F-3 oxygen analyzer in conjunction with a Heath recorder, model #EUW-20M (Fig. 3). The respiratory chamber consisted of a blacked-out gallon jar, which was made airtight by a seal of stopcock grease. The lid was fitted with three ports: one served as an air intake, another as an air outlet, and a third was an opening for a thermocouple. A wire mesh screen was fitted in the bottom of the chamber on which the bird rested. A constant ambient temperature $\pm 1^\circ$C was achieved by immersing the respiratory chamber in a circulating Aminco water bath. Air temperature of the chamber was monitored using a constantan thermocouple attached to a Leeds and Northrup Speedomax potentiometer (Fig. 3). Air was introduced into the respiratory chamber at a rate of 1000 cc/min and was dried over drierite (W. A. Hammond Drierite Co.) prior to entering and after leaving the chamber. Air entered the
Figure 3. Laboratory equipment used in determining oxygen consumption with oxygen analyzer and recorder, water bath with submerged respiratory chamber, and potentiometer.
oxygen analyzer at a rate of 150 cc/min.

To insure an accurate measurement of oxygen consumption at a given temperature, chickadees remained in the chamber for an average of two hours except at 40°C. The birds were allowed to adjust to the chamber for 90 minutes before any measurements were taken. The value used in determining oxygen consumption was that taken after a steady state of constant oxygen consumption was attained and then maintained for a period of 20 to 30 minutes. This level was usually reached after the animal was in the chamber for 75 minutes. Because of the stress imposed on the chickadees by handling and temperature, only birds that had been used at lower temperatures were used at 40°C. As soon as a steady state was reached after the first half-hour, a measurement was taken. The whole time period that the animal was in the respiratory chamber at 40°C was carefully controlled not to exceed 75 minutes.

Birds were weighed to the nearest 0.1 gram before and after each run; an average of these two values was used in calculating metabolic rate. The equipment was monitored each half hour to insures that a constant air flow and chamber temperature were maintained. Since the oxygen analyzer was sensitive to barometric pressure and air temperature of the laboratory, any changes in these conditions were noted at these times and the oxygen analyzer was recalibrated if necessary. Air temperature and pressure
were corrected to STP. To calculate heat production, a respiratory quotient of 0.75 and a caloric equivalent for oxygen of 4.74 gram calories per cubic centimeter were used (Dawson, 1954; Lustick, 1970).

Oxygen Consumption (24 Hour).

Daily metabolic activity was measured over a twenty-four-hour period at 10° and 25°C by determination of oxygen consumption, using a procedure similar to that described above. A clear, plexiglass metabolic chamber (25.5 x 20.5 x 20.5 cm) was employed in which an ample supply of food and water was placed with the bird. Three perches were positioned in the chamber so that conditions approximated a normal caged situation for the bird. The bottom of the chamber was lined with absorbent paper. The opening to the chamber (13 x 13 cm) was covered by a glass plate, three millimeters in thickness and sealed with stopcock grease. Temperature was monitored through a port in the same manner described above.

Each run commenced at 1100 and terminated at 1000 hours the next day. Since the runs were performed in a laboratory with windows, photoperiod had to approximate the natural conditions and therefore was timed from 0630 to 1830 hours. Equipment and climatic conditions of the laboratory were monitored every two hours during the day and every four hours during times of darkness. A screen was placed around
the waterbath to shield the chamber from human activity in the laboratory.

**Body Temperature**

Cloacal temperatures were measured at ambient temperatures from 0°C to 40°C at five-degree intervals using a Schultheis quick-acting thermometer (Schultheis and Sons, Arkville, N.Y.) to determine thermal conductance. The environmental room was adjusted for the desired temperature and the birds were allowed a two-hour period before any body temperatures were taken. All cages were covered prior to the two-hour period to avoid undue stress.

**Evaporative Water Loss**

Evaporative water loss was determined simultaneously with oxygen consumption (2 hour) after the chickadees had attained a steady state of minimal oxygen consumption. Air, as it left the respiratory chamber, was introduced into a small tube of drierite, which was inserted in the air-outlet line for 20 minutes. The drierite absorbed any water given off by the birds, the amount of which was determined by weighing the tube before and after each run. A Mettler H20T balance was used to weigh the drierite to the nearest 0.01 mg. About 200 ml of mineral oil was placed in the bottom of the respiratory chamber. The oil served to cover any feces voided during the experiment, thus preventing any water, other than that evaporated from
the respiratory surface, from entering the system. Relative humidity was determined by the formula presented by Lasiewski, Acosta, and Bernstein (1966).

**Ad Libitum and Minimum Water Consumption**

Water consumption was measured using the environmental walk-in chamber at temperatures of 20°C during the day and 15°C during the night. To standardize diet more closely, wild bird seed and sunflower seed only were made available. The measuring device consisted of a 25-ml graduated cylinder, fitted with a rubber stopper and an "L" shaped drinking tube. The drinking tube was made from glass Pyrex tubing (13 cm long) with a diameter of 11 mm. The whole device was fastened to the outside of the cage with the horizontal arm of the tube extending 15 mm into the cage and from which a small hole (6 mm in diameter) opened. Most chickadees readily learned to use the tube when deprived of their normal 60-ml watering cups. Drinking tubes were made available to the birds at least a month before studies began. Watering cups were first removed for a four-hour period, then for an eight-hour period before the birds were completely deprived of the open jar-type cups. This process lasted about two weeks.

*Ad libitum* water consumption was determined over a period of seven days by filling the graduated cylinder to the 25 ml mark. Birds were weighed on alternate days.
During this time. After seven days the water regime was reduced to 10 ml, and the birds were weighed daily thereafter. Birds were maintained on a particular water regime for several days; when body weight stabilized or increased, the water ration was decreased. This process was continued until a point was reached when an individual bird could no longer stabilize its weight on the given amount of water provided. If body weight steadily decreased over a period of three days, the amount of water provided was determined to be the daily minimum requirement. The entire process usually required a total of 30 to 40 days. After minimum water consumption was determined, water was again provided ad libitum. All weighing and water measurements were made immediately at the start of the photoperiod (0800 hours).

To correct for evaporation, a control drinking tube was set outside the cages. Relative humidity was recorded three times a day using an Electric Hygrometer Indicator (Hygrodynamics, Inc.). For all measurements taken over a 60-day period, the average daily humidity was 57%, although this ranged from 99 to 20 percent at various times.

Oxygen Consumption and Artificial Radiation

The equipment used in this procedure was similar to that employed for measuring oxygen consumption over a 24-hour period. The same plexiglass chamber was placed in the
waterbath which was set to maintain an air temperature of 5°C, a temperature determined to be below the thermoneutral zone. No food or water was provided and only a single perch was placed in the chamber; the perch was centered in the chamber about one millimeter above the chamber floor. Since a diurnal standard metabolic rate was desired, the chickadees were fasted for two hours, weighed, placed in the chamber for a two-hour period, weighed, and released to their cages. This procedure was followed under normal daylight and laboratory conditions on one day and two days later under conditions of artificial radiation. The same birds were used in each instance and at approximately the same time each day. Body temperature was also recorded after each two-hour period.

The radiation source consisted of a General Electric R-40, 250 watt, clear end infrared lamp (color temperature 2500°K) placed directly over the glass window and 40 cm above the floor of the chamber. The light received by the animal had a spectral range of 400 to 1400 nm, the approximate wavelength of solar radiation. This was insured by having the chamber covered by one centimeter of water which eliminated all wavelengths above 1400 nm (Ruttner, 1963). A Belfort pyro-heliometer recorded approximately 0.9 cal/cm²/min at a height of seven centimeters above the floor of the submerged chamber. Air temperature was monitored using
the Leeds and Northrup potentiometer and a constantan thermocouple which was shielded from direct radiation by an opaque, inverted plastic cup.

In addition to oxygen consumption and body temperature, the activity levels of several birds exposed to normal daylight and artificial radiation were measured separately after the metabolic studies were concluded. This was accomplished by placing two straight lever microswitches (Micro-Switch, Freeport, Illinois) (model #BZ-2RW80) on the bottom of the plexiglass chamber. Perches, attached to the levers, were the only places in the chamber where the birds could rest, and therefore the movement of the birds from perch to perch caused the microswitches to be depressed under the weight of the birds. The microswitches were connected to an Esterline Angus Event Recorder, model #S-620, which recorded the activity. The airline was attached to the chamber and the apparatus was then placed in the circulating water bath under the same conditions as noted above. A bird was left in the chamber for a total of two hours, receiving ordinary light for the first hour and artificial radiation for the second hour.
RESULTS

General Observations

During the course of the study, collection efforts were made in central Ohio for both Black-capped and Carolina Chickadees. No Black-caps were found in any of the central Ohio study areas. Carolinas appeared individually at feeders or in small flocks of mixed species. These flocks included White-breasted Nuthatch (*Sitta carolinensis*), Tufted Titmouse (*Parus bicolor*), Cardinal (*Cardinalis cardinalis*), Dark-eyed Junco (*Junco hyemalis*), and to a lesser extent Downy Woodpecker (*Dendrocopus pubescens*), Red-breasted Nuthatch (*Sitta canadensis*), and White-throated Sparrow (*Zonotrichia albicollis*), all of which were either netted or trapped. In the northern and southern Ohio study areas, chickadees traveled in flocks which were made up almost exclusively of their own species.

Field behavior toward humans was dramatically different between the two species. Black-capped Chickadees approached the feeders with little hesitation with or without a human in close proximity. When a Black-cap was captured and caged, one or two Black-caps alighted on the holding cage in a tenacious manner that has often been
ascribed to this species (Chapman, 1934; Forbush and May, 1939; Todd, 1940). This type of behavior was not typical of the Carolina in the field, although both species displayed a considerable degree of aggressiveness when handled under caged conditions. Both species adapted well to caged conditions and learned to use feeding devices with little problem, a characteristic that seems to be typical of the parids (Austin, 1961).

The experiment to determine whether chickadees use nesting cavities showed that the birds do not necessarily use nest holes at night. Occasionally a bird would rest in a depression on the top of a stump. Birds were observed roosting near the stumps, but except for the one Carolina at 15°C, no birds utilized nest holes at night.

Weight

One of the criteria in establishing morphological difference between the Carolina and Black-capped Chickadees is the degree of difference in body proportions and weight. Weight is a parameter used in determining metabolic rate, and since it was always measured under the same conditions, a comparison between the species was made. Weight of a bird varied depending on the time of day, the length of time in captivity, and the amount of stress placed on it by an individual experiment or series of experiments. For this reason, the figure first used in the analysis was the
fasted daytime weight, i.e. the weight recorded from the first experiment conducted on an individual specimen.

Fasted daytime weight results are summarized in Table 2 and presented in Fig. 4. The difference between mean weight of the two species was 1.2 g. When a student's "t" test was applied to the data, the difference in weight between the two species was found to be significant (P < 0.05). Since the Carolina Chickadees were obtained from two different locations in Ohio, tests for confidence interval and significance were run. No significance existed between the two samples (P > 0.05).

Most weight studies in the literature record field weight and because of this a second analysis was done for comparison. Field weight was the first weight recording taken after capture. The difference in mean field weight of the two species was 1.6 g, which is also significant (P < 0.05). The difference in field weight for the two Carolina populations was significant (P < 0.05). Results of the field weight analysis are summarized in Table 3 and presented in Fig. 4 with the results for fasted weight.

Oxygen Consumption (2 Hour)

Diurnal oxygen consumption: Black-capped vs. Carolina Chickadee. The relationship between diurnal oxygen consumption and ambient temperature over the temperature range of 0°C to 40°C for the Black-capped Chickadee is shown in
### TABLE 2

**FASTED WEIGHT ANALYSIS**

<table>
<thead>
<tr>
<th>All Birds</th>
<th>Number of Birds</th>
<th>Mean Weight (g)</th>
<th>Standard Error</th>
<th>95% Confidence Interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black-capped Chickadee</td>
<td>36</td>
<td>11.09</td>
<td>0.11</td>
<td>11.31  10.87</td>
</tr>
<tr>
<td>Carolina Chickadee</td>
<td>33</td>
<td>9.89</td>
<td>0.15</td>
<td>10.20  9.59</td>
</tr>
</tbody>
</table>

| Carolina Chickadees       |                 |                 |                |                         |
| Delaware Co.              | 23              | 9.86            | 0.18           | 10.23  9.49             |
| Clermont Co.              | 10              | 9.94            | 0.31           | 10.64  9.24             |
## TABLE 3
### FIELD WEIGHT ANALYSIS

<table>
<thead>
<tr>
<th></th>
<th>Number of Birds</th>
<th>Mean Weight (g)</th>
<th>Standard Error</th>
<th>95% Confidence Interval</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Upper Limit</td>
</tr>
<tr>
<td><strong>All Birds</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black-capped Chickadee</td>
<td>72</td>
<td>11.83</td>
<td>0.15</td>
<td>12.13</td>
</tr>
<tr>
<td>Carolina Chickadee</td>
<td>59</td>
<td>10.23</td>
<td>0.08</td>
<td>10.39</td>
</tr>
<tr>
<td><strong>Carolina Chickadees</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Delaware Co.</td>
<td>37</td>
<td>10.11</td>
<td>0.10</td>
<td>10.31</td>
</tr>
<tr>
<td>Clermont Co.</td>
<td>22</td>
<td>10.44</td>
<td>0.11</td>
<td>10.67</td>
</tr>
</tbody>
</table>
Figure 4. A comparison between body weight of the Black-capped Chickadee (BCC) and Carolina Chickadee (CC) under fasted and field conditions. Vertical lines represent the range, circles the means, and horizontal lines the 95% confidence limits ("t" x SEM). Del. and Cl. represent Delaware and Clermont Counties. Numbers of birds used in each determination may be found in Tables 2 and 3.
WEIGHT (g)

BCC CC  BCC CC  DEL. CL.  DEL. CL.
FASTED WT. FIELD WT. FASTED WT. FIELD WT.

ALL BIRDS  C C
Fig. 5. The thermal neutral zone for this species apparently extends from $25^\circ$ to $35^\circ$C, the range in which oxygen consumption and individual variation are normally minimal. The lower limit of the zone is not as well defined as the upper limit, however the points within the thermal neutral zone were not significantly different from zero when tested (t-test for deviation from 0 between two slopes) ($P>0.05$). Between these temperatures the oxygen consumption increased at a rate of $0.037 \, \text{cc}O_2/\text{g}/\text{hr}/^\circ\text{C}$ with decreasing ambient temperature. Between $25^\circ$ and $0^\circ$C, oxygen consumption increased at a rate of $0.215 \, \text{cc}O_2/\text{g}/\text{hr}/^\circ\text{C}$ in a linear manner. A line fitted by the method of least squares is described by the equation:

$$y = 10.79 - 0.215X$$

with a correlation coefficient of $-0.72$.

The zone of thermoneutrality for the Carolina Chickadee extended over the same temperature range (Fig. 6). Although the points within this range did not differ significantly from zero when tested, the lower limit of the thermal neutral zone was more defined than for the Black-capped Chickadee. The rate of increasing oxygen consumption was $0.029 \, \text{cc}O_2/\text{g}/\text{hr}/^\circ\text{C}$ as temperature decreased. Below $25^\circ$C the rate of increase was $0.292 \, \text{cc}O_2/\text{g}/\text{hr}/^\circ\text{C}$ as described by a linear regression line having the equation:

$$y = 11.70 - 0.292X$$
Figure 5. The diurnal standard oxygen consumption of the Black-capped Chickadee in relation to ambient temperature. Vertical lines represent the range, circles the means, and horizontal lines the 95% confidence limits ("t" x SEM). Numbers of birds measured at each temperature ranged from 6 to 9.
and a correlation coefficient of -0.87. The two regression lines were compared using an analysis of covariance (Snedecor and Cochran, 1967). The results of this test showed no significant difference (P>0.05) between the two species in the amount of oxygen consumed (i.e. elevation of the line) or in the rate of oxygen consumption increase as ambient temperature decreased (i.e. slope of the line).

Nocturnal oxygen consumption: Black-capped vs. Carolina Chickadee. The results for nocturnal oxygen consumption are found in Figs. 7 and 8 for the Black-capped and Carolina Chickadees respectively. Instead of a distinct thermal neutral zone, the Black-capped Chickadee was found to have a thermal neutral point at 30°C. The Carolina Chickadee had a well-defined thermal neutral zone between 25°C and 35°C, and when the points within this range were tested for deviation from zero, no significance was noted (P>0.05). The increase of oxygen consumption with temperature decrease was 0.002 ccO₂/g/hr/°C.

Below 30°C, the oxygen consumption increased with decreasing ambient temperature at a rate of 0.177 ccO₂/g/hr/°C for the Black-capped Chickadee and produced a linear regression line expressed by the equation

\[ y = 8.86 - 0.177X. \]

The correlation coefficient was -0.84. The rate of oxygen consumption increase for the Carolina Chickadee was 0.168
Figure 6. The diurnal standard oxygen consumption of the Carolina Chickadee in relation to ambient temperature (symbols as in Fig. 5). Numbers of birds measured at each temperature ranged from 6 to 9.
Figure 7. The nocturnal standard oxygen consumption of the Black-capped Chickadee in relation to ambient temperature (symbols as in Fig. 5). Numbers of birds measured at each temperature ranged from 6 to 8.
ccO₂/g/hr/°C and the equation for the regression line was
\[ y = 8.24 - 0.168X. \]
The correlation coefficient was -0.83. When an analysis of covariance was performed on these two lines, no significance was found to exist (P>0.05) between the data for the rate of oxygen consumption increase below the lower limit of thermoneutrality. A difference was found between the species for the amount of oxygen consumed at the temperatures below thermoneutrality, which indicates a lower nocturnal metabolic rate in the Carolina Chickadee.

Black-capped Chickadee: Diurnal vs. nocturnal oxygen consumption. The above data were also used in making intraspecific comparisons. Diurnal and nocturnal oxygen consumption at temperatures below thermoneutrality were compared by analysis of covariance of the regression lines. No significant difference (P>0.05) in the slope of the lines indicates that the rate of oxygen consumption with decreasing ambient temperature at night was the same as during the day. A significant difference (P<0.05) was found to exist in the elevation of the lines, which showed the demand for oxygen to be lower at night than in the day.

Carolina Chickadee: Diurnal vs. nocturnal oxygen consumption. When the same comparisons were made for the Carolina Chickadee, oxygen consumption was also shown to be significantly lower at night. A significant difference
Figure 8. The nocturnal standard oxygen consumption of the Carolina Chickadee in relation to ambient temperature (symbols as in Fig. 5). Numbers of birds measured at each temperature ranged from 6 to 8.
(P≤0.05) in the slope of the lines indicated a slower rate of oxygen consumption at night with decreasing ambient temperature.

Oxygen Consumption (24 Hour)

Four Black-capped Chickadees and four Carolina Chickadees were run at 25°C, a temperature within the zone of thermoneutrality, and two individuals of each species were run at 10°C, a temperature well below thermoneutrality. All birds maintained a daily cycle of activity similar to that observed in the holding cages. When birds became quiescent for any length of time at 10°C, they tended to fluff their feathers. Figs. 9 and 10 present the results obtained and illustrate the difference between the fasting nocturnal condition and the daytime active state of the birds. Both species displayed a similar rhythm of metabolic rate whether at 25°C or 10°C.

Tables 4 and 5 compare the average diurnal and nocturnal rates of oxygen consumption of each individual at 25°C and 10°C respectively. Data for body temperature and the standard metabolic rate obtained using the darkened respiratory chamber are included for comparison.

Body Temperature

The body temperature of chickadees was determined by taking the mean of at least six specimens of each species. Body temperature was taken over a two-week period at the
Figure 9. The 24 hour record of oxygen consumption for the Black-capped Chickadee (solid line) and Carolina Chickadee (dashed line) at 25°C. Four birds of each species were used in these measurements. Additional data is contained in Table 4.
Figure 10. The 24 hour record of oxygen consumption for the Black-capped Chickadee (solid line) and Carolina Chickadee (dashed line) at 10°C. Two birds of each species were used in these measurements. Additional data is contained in Table 5.
## TABLE 4

AVERAGE DIURNAL AND NOCTURNAL OXYGEN CONSUMPTION OVER 24 HOURS AT 25°C

<table>
<thead>
<tr>
<th>Bird #</th>
<th>Species</th>
<th>Average Oxygen Consumption (ccO₂/g/hr)</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Diurnal</td>
<td>Nocturnal</td>
</tr>
<tr>
<td>BA59</td>
<td>Black-capped</td>
<td>8.82</td>
<td>4.82</td>
</tr>
<tr>
<td>BA62</td>
<td>Black-capped</td>
<td>7.41</td>
<td>4.22</td>
</tr>
<tr>
<td>BA66</td>
<td>Black-capped</td>
<td>7.46</td>
<td>4.30</td>
</tr>
<tr>
<td>BA67</td>
<td>Black-capped</td>
<td>6.65</td>
<td>3.44</td>
</tr>
<tr>
<td>CC49</td>
<td>Carolina</td>
<td>6.93</td>
<td>3.98</td>
</tr>
<tr>
<td>CC54</td>
<td>Carolina</td>
<td>7.47</td>
<td>4.90</td>
</tr>
<tr>
<td>CC58</td>
<td>Carolina</td>
<td>8.26</td>
<td>4.33</td>
</tr>
<tr>
<td>CC59</td>
<td>Carolina</td>
<td>6.28</td>
<td>4.54</td>
</tr>
</tbody>
</table>

### AVERAGE FASTING OXYGEN CONSUMPTION (ccO₂/g/hr) AT 25°C IN RESPIRATORY CHAMBER (2 hr)

<table>
<thead>
<tr>
<th>Species</th>
<th>Average Oxygen Consumption (ccO₂/g/hr)</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Black-capped</td>
<td>4.98</td>
<td>4.99</td>
</tr>
<tr>
<td>Carolina</td>
<td>4.49</td>
<td>4.08</td>
</tr>
</tbody>
</table>

### AVERAGE BODY TEMPERATURE AT 25°C

<table>
<thead>
<tr>
<th>Species</th>
<th>Average Body Temperature</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Black-capped</td>
<td>40.1</td>
<td>38.0</td>
</tr>
<tr>
<td>Carolina</td>
<td>39.6</td>
<td>38.3</td>
</tr>
</tbody>
</table>
### TABLE 5

**AVERAGE DIURNAL AND NOCTURNAL OXYGEN CONSUMPTION OVER 24 HOURS AT 10°C**

<table>
<thead>
<tr>
<th>Bird #</th>
<th>Species</th>
<th>Average Oxygen Consumption (ccO\textsubscript{2}/g/hr)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Diurnal</td>
</tr>
<tr>
<td>BA59</td>
<td>Black-capped</td>
<td>12.29</td>
</tr>
<tr>
<td>BA70</td>
<td>Black-capped</td>
<td>11.62</td>
</tr>
<tr>
<td>CC46</td>
<td>Carolina</td>
<td>11.01</td>
</tr>
<tr>
<td>CC63</td>
<td>Carolina</td>
<td>9.71</td>
</tr>
</tbody>
</table>

**AVERAGE FASTING OXYGEN CONSUMPTION (ccO\textsubscript{2}/g/hr) AT 10°C IN RESPIRATORY CHAMBER (2 hr)**

<table>
<thead>
<tr>
<th>Species</th>
<th>Diurnal</th>
<th>Nocturnal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black-capped</td>
<td>8.20</td>
<td>7.55</td>
</tr>
<tr>
<td>Carolina</td>
<td>8.47</td>
<td>6.44</td>
</tr>
</tbody>
</table>

**AVERAGE BODY TEMPERATURE AT 10°C**

<table>
<thead>
<tr>
<th>Species</th>
<th>Diurnal</th>
<th>Nocturnal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black-capped</td>
<td>38.1</td>
<td>36.5</td>
</tr>
<tr>
<td>Carolina</td>
<td>36.9</td>
<td>35.2</td>
</tr>
</tbody>
</table>
same ambient temperatures as those used in determining standard metabolic rate. Diurnal temperatures were taken between 1200 and 1600 hours; nocturnal temperatures were recorded between 2200 and 0200 hours.

A student's "t" test was used to compare the data between the species and within each species. Generally, no significant difference was found between the two species (P>0.05). This was true for both day and night values (Figs. 11 and 12).

When the same test was applied to the data within each species a significant difference was found between day and night values (P<0.05). (Figs. 13 and 14).

The similarity of each species in body temperature can also be noted from the data presented in Table 6. The mean body temperature in thermoneutrality is approximately the same for both species. Decrease in body temperature from an ambient temperature of 25°C to 0°C is approximately 0.165°C for each degree drop in ambient temperature, except for the Carolina Chickadee at night which dropped its body temperature 0.3°C for each degree drop in ambient temperature. If the linear approximation to overall heat transfer (Bakken and Gates, 1974), i.e. the adaptation by Scholander et al. (1950) of Newton's law of cooling, is assumed below the ambient temperature of thermoneutrality, the line fitted to oxygen consumption (Figs. 5 to 8), when extrapolated, intercepts ambient temperature between 40°C and 42°C,
Figure 11. A comparison between the Black-capped Chickadee (solid lines) and Carolina Chickadee (dashed lines) diurnal body temperature in relation to ambient temperature (symbols as in Fig. 5). Numbers of birds measured at each ambient temperature ranged from 6 to 8.
Figure 12. A comparison between the Black-capped Chickadee (solid lines) and Carolina Chickadee (dashed lines) nocturnal body temperature in relation to ambient temperature (symbols as in Fig. 5). Numbers of birds measured at each temperature ranged from 6 to 8.
Figure 13. A comparison between the diurnal (solid lines) and nocturnal (dashed lines) body temperature of the Black-capped Chickadee in relation to ambient temperature (symbols as in Fig. 5). Numbers of birds measured at each temperature ranged from 6 to 8.
Figure 14. A comparison between the diurnal (solid lines) and nocturnal (dashed lines) body temperature of the Carolina Chickadee in relation to ambient temperature (symbols as in Fig. 5). Body temperature was measured on 6 birds at each ambient temperature.
<table>
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<tr>
<th>Species</th>
<th>Mean $T_B$ in Thermoneutrality</th>
<th>Decrease $T_B/°C$ from 25-0°C</th>
<th>Extrapolated $T_B$</th>
<th>Mean $T_B$ from 0-40°C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black-capped</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day</td>
<td>40.14</td>
<td>0.16</td>
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<tr>
<td>Night</td>
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<td>0.18</td>
<td>42.0</td>
<td>37.30</td>
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<td>Carolina</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day</td>
<td>40.09</td>
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<td>40.0</td>
<td>38.60</td>
</tr>
<tr>
<td>Night</td>
<td>39.07</td>
<td>0.30</td>
<td>41.5</td>
<td>36.68</td>
</tr>
</tbody>
</table>
which approximates normal body temperature. Interspecific difference in mean body temperature over the whole range of ambient temperatures (0° to 40°C) was approximately one-half degree. Intraspecific difference between day and night was about two degrees.

**Evaporative Water Loss**

At the same time that oxygen consumption was measured, evaporative water loss was also determined (Figs. 15 and 16). When a student's "t" test was applied to the data, no significant difference was found (P>0.05). This was true in comparing Black-capped with Carolina Chickadees as well as making intraspecific comparisons between day and night data. In most cases evaporative water loss was fairly constant between 0° and 25°C, increasing markedly between 30° and 40°C. Although this increase was significant from 25° to 35°C (P≤0.05) (except for the Carolina Chickadee at night where a significant increase was from 30° to 35°C), water loss at the higher temperatures of 35° and 40°C was not as high as has been generally accepted for small birds (Cade, 1964; Lasiewski, Acosta, and Bernstein, 1966). The increase in water loss at these temperatures was approximately one and a half times that found at the lower ambient temperatures.

Based on an RQ of 0.75, one cubic centimeter of oxygen consumed is equivalent to 4.74 calories of heat produced.
Figure 15. A comparison between the Black-capped Chickadee (solid lines) and Carolina Chickadee (dashed lines) diurnal evaporative water loss and mean heat loss in relation to ambient temperature (symbols as in Fig. 5). The boxes represent the mean heat lost by evaporation in percent. Numbers of birds measured at each temperature ranged from 6 to 8.
Figure 16. A comparison between the Black-capped Chickadee (solid lines) and Carolina Chickadee (dashed lines) nocturnal evaporative water loss and mean heat loss in relation to ambient temperature (symbols as in Figs. 5 and 15). Numbers of birds measured at each temperature ranged from 6 to 8.
Since one gram of water requires 574 calories (at a temperature of 40°C) to be evaporated, the percentage of heat lost by evaporation can be calculated. This was accomplished using the following formula:

\[ 100 \times \frac{\text{mg water produced/g/hr} \times 574 \text{ cal}}{\text{CO}_2 \text{ consumed/g/hr} \times 4.74 \text{ cal}} \]

During the day, the birds were able to lose between 20 and 25% of the heat produced by evaporative water loss (Fig. 15) at 40°C. At night, this figure decreased to about 17.5% (Fig. 16). Relative humidity of the respiratory chamber was calculated by using the formula:

\[ \% \text{RH} = 100 \times \frac{x/y}{z} \]

where \(x\) is the amount of water vapor added to the air by the bird in mg/min, \(y\) is the air flow in l/min, and \(z\) is the density of saturated steam at ambient temperature obtained from the Handbook of Chemistry and Physics (Lasiewski, Acosta, and Bernstein, 1966). From relative humidity, water-vapor pressure was determined. Mean water-vapor pressure for daytime readings were as follows: below thermoneutrality, 0.95; in thermoneutrality, 1.27; above thermoneutrality (40°C), 2.05. The water-vapor pressure at night was 0.71 below 40°C and 1.72 for 40°C.

**Thermal Conductance**

Thermal conductance was determined from the data obtained from the studies on oxygen consumption and body
temperature as described above. This was calculated using the adaptation by Scholander et al. (1950) of the linear approximation to heat transfer (Bakken and Gates, 1974), which states:

\[ MR = C(T_B - T_A) \text{ or } C = \frac{MR}{T_B - T_A} \]

where \( MR \) = cc\( \text{O}_2 \) consumed/g/hr, \( T_A \) and \( T_B \) = temperature in degrees centigrade. In both day and night determinations for both species, these values remained fairly constant for temperatures below 30° C (Figs. 17 to 20). Values increased significantly from 30° to 35° C (\( P \leq 0.05 \)), approximately doubling thermal conductance for lower temperatures. As ambient temperature increased approaching body temperature, thermal conductance increased and became asymptotic at an ambient temperature of 40° C.

When a student's "t" test was run to compare the data, no significance was found between species either during the day or at night (\( P > 0.05 \)). Intraspecifically, there was a difference between day and night thermal conductance. Below thermoneutrality, i.e. 0 – 20° C, the difference in thermal conductance was significantly lower at night (\( P \leq 0.05 \)). In the thermal neutral zone, no significant difference in thermal conductance between day and night was found for the Carolina (\( P > 0.05 \)). Thermal conductance at night was significantly different (\( P \leq 0.05 \)) from the day in the Black-capped, reflecting the low nocturnal metabolic rate at 30° C.
Figure 17. A comparison between the Black-capped Chickadee (solid lines) and Carolina Chickadee (dashed lines) diurnal thermal conductance and mean dry heat loss in relation to ambient temperature (symbols as in Fig. 5). The boxes represent the mean dry heat loss (thermal conductance - evaporative water loss). Numbers of birds measured at each temperature ranged from 6 to 9.
Figure 18. A comparison between the Black-capped Chickadee (solid lines) and Carolina Chickadee (dashed lines) nocturnal thermal conductance and mean dry heat loss in relation to ambient temperature (symbols as in Figs. 5 and 17). Numbers of birds measured at each temperature ranged from 6 to 8.
Figure 19. A comparison between the diurnal (solid lines) and nocturnal (dashed lines) thermal conductance of the Black-capped Chickadee in relation to ambient temperature (symbols as in Fig. 5). Numbers of birds measured at each temperature ranged from 6 to 8.
Figure 20. A comparison between the diurnal (solid lines) and nocturnal (dashed lines) thermal conductance of the Carolina Chickadee in relation to ambient temperature (symbols as in Fig. 6). Numbers of birds measured at each temperature ranged from 6 to 8.
Since thermal conductance is generally defined as the rate of heat change per degree difference between an object and its surroundings (Bartholomew, 1968), thermal conductance as presented in Figs. 17 to 20 incorporates all methods of heat gain or loss, including evaporative water loss. If the amount of heat lost by evaporation is eliminated from thermal conductance, the dry heat flow can be calculated, which provides an estimate of heat transfer by methods such as conduction, convection, and radiation. Dry heat flow (Figs. 17 and 18) was calculated from an adaptation of an equation provided by Dawson and Schmidt-Nielsen (1966):

\[ C = \frac{\text{MR} - \text{He}}{T_B - T_A} \]

Metabolic rate (MR) and heat lost by evaporation (He) were both calculated in terms of calories, and then the quotient recalculated in terms of ccO\(_2\) consumed/g/hr/°C on the basis that one cubic centimeter of oxygen produced 4.74 calories. The dry heat flow followed a pattern similar to that of thermal conductance over the temperature range of 0° to 35°C. The mean dry heat flow was generally less than the mean thermal conductance. At 35°C the dry heat flow was approximately double that of the temperatures below thermoneutrality. At 40°C, mean body temperature exceeded ambient temperature, and this, combined with a low evaporative water loss, resulted in a high dry heat flow from the bird to the
environment (Figs. 17 and 18). On a caloric basis, dry heat flow during the day was calculated to be more than twice the evaporative water loss and at night more than five times the evaporative water loss.

Ad Libitum and Minimum Water Consumption

The results of water consumption studies at 20°C are found in Tables 7 and 8. Occasionally a bird was found to have drunk all 25 ml of water, an occurrence noted by others also (Calder, 1964). Since cage floors were sometimes found to be damp when this occurred, some birds were probably removing water by splashing rather than actual drinking. Values for splashing or excessive drinking were eliminated from calculations. Mean ad libitum water consumption (± standard error of the mean) for the Black-capped Chickadee was 5.6 ml ± 1.2 and 5.9 ml ± 1.3 for the Carolina Chickadee. Expressed as percent body weight, the Black-capped drank 52.8% of its body weight and the Carolina drank 53.6%. The difference between these values was not significant when compared using a student's "t" test (P>0.05).

Minimum water consumption (± standard error of the mean) was determined as 2.3 ml ± 0.5 for the Black-capped and 2.8 ml ± 1.9 for the Carolina. Using the same test as above, the difference between the species is not significant (P>0.05). The mean weight loss of birds on minimum water
<table>
<thead>
<tr>
<th>Bird</th>
<th>Ad Lib.</th>
<th>Minimum</th>
<th>Initial</th>
<th>Minimum</th>
<th>% Weight Lost</th>
<th>Weight (g) After 24 Hr.</th>
<th>Weight (g) After 48 Hr.</th>
<th>Maximum Days To Weight Min. Water</th>
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<tr>
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<td>6.96</td>
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<td>11.67</td>
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<td>29.5</td>
<td>8.76</td>
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<td>9.61</td>
<td>10.68</td>
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* Bird died shortly after study was concluded; weight was not included in mean.
### TABLE 8
RESULTS FROM STUDIES ON AD LIBITUM AND MINIMUM WATER: CAROLINA CHICKADEE

<table>
<thead>
<tr>
<th>Bird</th>
<th>Water (ml)</th>
<th>Weight (g)</th>
<th>% Weight Lost</th>
<th>Weight (g) After 24 Hr.</th>
<th>Weight (g) After 48 Hr.</th>
<th>Maximum Weight</th>
<th>Days To Min. Water</th>
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<td>10.19</td>
<td>7.33</td>
<td>7.33*</td>
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<td>10.64</td>
<td>8.56</td>
<td>19.5</td>
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<td>9.92</td>
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<td>16.9</td>
<td>8.88</td>
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</tr>
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<td>27.4</td>
<td>8.09</td>
<td>7.96</td>
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<td>23.0</td>
<td>8.44</td>
<td>8.79</td>
<td>9.99</td>
</tr>
</tbody>
</table>

* Bird died shortly after study was concluded; weight was not included in mean.
was 16.6% for the Black-capped and 23.0% for the Carolina, which was determined to be insignificant (P>0.05). When the minimum water studies were concluded, ad libitum water was restored and daily weight records were maintained for approximately ten days thereafter. Four birds were weighed six hours (1400 hours) after ad libitum water was made available and were noted to have increased their weight an average of 5% (0.5g) over their initial weight. All birds' weights returned to near or better than the initial weight after 48 hours of rehydration (Tables 7 and 8). A maximum weight of all surviving birds was reached approximately six days after the minimum water studies were concluded. Weight increases ranged from 0.1 to 2.1 grams for five of the seven birds.

Oxygen Consumption and Artificial Radiation

At 5°C, exposure of the birds to artificial radiation decreased oxygen consumption by eight and ten percent for the Black-capped and Carolina Chickadees respectively (Fig. 21). The decrease in metabolic rate under conditions of artificial radiation was not significant for either species when a paired "t" test was used to compare the data (P > 0.05). Mean body temperature, measured immediately after the birds were removed from the chamber, showed approximately a two degree increase (Fig. 21) under conditions of artificial radiation. Although the data indicate solar
radiation may contribute to the maintenance of a higher body temperature at lower ambient temperatures, a paired "t" test revealed no significant difference between those chickadees receiving artificial radiation and those not receiving artificial radiation (P>0.05). The results from activity level studies were variable and did not show any apparent trend. When tested by the same method, no significance was noted.
Figure 21. A comparison of the oxygen consumption between Black-capped Chickadees (BCC) and Carolina Chickadees (CC) receiving artificial solar radiation (dashed lines) and those not receiving artificial solar radiation (solid lines) (symbols as in Fig. 5) at 5°C. Six birds of each species were used.
DISCUSSION

Weight

Although the appearance of the species is similar, small variations in color, wing chord, and tail length do exist (see Trautman, 1966; Reilly, 1968; Wood, 1969). The same is significantly true of the fasted daytime and field weights of the species. The Black-capped Chickadee has a mean fasted weight of approximately 11.1 g and a field weight of 11.8 g. When compared with other data, the Black-capped follows the trend of increasing in weight from south to north (Bergman's rule). The weight data from this research on Black-caps taken in Ohio (41.5° N. Lat.) is similar to the work of Baldwin and Kendeigh (1938) in Ohio (41.3° N. Lat.), which produced a mean weight of 11.1 g during the same time of the year (October to March). Over the same time period, Lawrence (1958) reported a mean weight of 11.9 g for Black-caps in Ontario (46° N. Lat.). Odum (1943) reported a mean weight of 12.2 g for New York Chickadees (42.3° N. Lat.), but the data cover a shorter time in terms of months.

Brewer (1961) found Carolina Chickadees to have a mean field weight of 10.1 g in Illinois (38.5° N. Lat.).
Analyzing his results and others from the literature, he found the same trend of increasing weight from south to north to exist for the Carolina. The results from the present study indicate that this is not always the case during the period October to March. The mean fasted weight of all Carolinas was found to be about 9.9 g; the mean field weight was 10.2 g. Fasted Carolinas from southern Ohio (Clermont Co., 39.1° N. Lat.) weighed 9.94 g, compared to chickadees from central Ohio (Delaware Co., 40.18° N. Lat.) which weighed 9.86 g. The field weight for these birds was 10.4 g and 10.1 g respectively. Over a similar time, Nice (1938) obtained an average weight of 10.55 g for Carolinas from central Ohio (Franklin Co., 39.5° N. Lat.). Wiseman (personal communication, 1974) reports that he has always found a heavier Carolina Chickadee in southern Ohio. From a sample of more than 1000 specimens, he has calculated the mean field weight to be 10.64 g; other body measurements are also comparably larger. Snow (1954a) refers to this as a "latitude effect" and notes that it may be more prominent in some species than in others. When he compared four species of Parus from southern Europe and northern Africa with their counterparts in northern lowlands, the southern populations were found to contain the heavier birds. The fasted weight difference in the Carolina populations of Ohio was not statistically significant, but indications are that
weight is more variable in the Carolina than in the Black-capped. Looking at the Black-capped and Carolina Chickadees together, a cline of increasing weight from south to north is apparent. Since Bergman's rule states that a species increases in size in northern latitudes, the cline-like effect of weight in chickadees would help support the concept of one chickadee species, rather than two, or the theory of recent evolutionary divergence of the two species. Scholander (1955) largely discounts Bergman's rule and argues that the overall size of an animal is of little consequence in the adaptation of animals to colder environments. More important than size are the physiological mechanisms of the animal, such as vascular heat exchangers, changes in body insulation, and adaptation of peripheral parts. Regardless of size, the results of the present study show that the chickadee, whether Black-capped or Carolina, is well-adapted to environments of colder temperatures.

**Oxygen Consumption**

The thermal neutral zone, the temperature range over which oxygen consumption is minimal, will vary depending on the species of homeotherm studied. Both the Black-capped Chickadee and Carolina Chickadee possess a similar thermal neutral zone, extending from 25° to 35°C. This approximates the general range of a hypothetical endotherm (Bartholomew, 1968) and is a rather broad zone for these birds considering
their small size. There is a paucity of data on thermo-
neutralitity of passerines this size, but several finch
species, approximately twice the size of chickadees, have
been studied. Salt (1952) obtained a thermal neutral zone
of five degrees or less on western finches, while Hudson
and Kimzey (1966) recorded that thermoneutrality extended
over a fifteen degree range for the White-throated Sparrow
and House Sparrow (Passer domesticus).

Several equations have been formulated from which the
metabolic rate of a bird may be predicted according to body
weight. When related to the Brody-Proctor, King-Farner,
and Lasiewski-Dawson equations (Lasiewski and Dawson, 1967),
the chickadee data closely agreed with the Lasiewski-Dawson
equation for passerines. The equation, which describes the
relationship between standard metabolic rate and body weight
in passerines, is as follows:

$$\log M = \log 129 + 0.724 \log W \pm 0.113$$

where $M$ is heat production in kcal/day and $W$ is body weight
in kg. Thus, a ten-gram chickadee produces about five kilo-
calories per day. In studies on Black-caps in New York,
Budd (1972) obtained predicted values also using the
Lasiewski-Dawson equation and calculated nocturnal oxygen
consumption to be 6.8 cc$O_2$/g/hr at 0°C. Nocturnal oxygen
consumption at 0°C for Ohio Black-caps was 8.8 cc$O_2$/g/hr.
Since there are no other data available, a statistical
comparison between data is not possible. However, the difference may be attributable to a combination of two factors. First, Budd's specimens were obtained from a more northern location, but, perhaps more important, her chickadees were winter acclimatized while specimens used in this research were acclimated to room temperature (ca. 20°C). Budd (personal communication, 1974) did a limited amount of work on Carolina Chickadees from the state of Delaware and found no dramatic differences in the metabolism curves between the two species.

Within thermoneutrality, the diurnal standard metabolic rate, which was 4.7 ccO₂/g/hr for the Black-capped and 4.5 ccO₂/g/hr for the Carolina, was slightly higher than the nocturnal rate of 3.2 and 4.1 ccO₂/g/hr for the Black-capped and Carolina respectively. The lower nighttime rate of oxygen consumption is also found to occur in other species such as the Great Tit, Parus major (Steen, 1958), House Sparrow, and White-throated Sparrow (Hudson and Kimzey, 1966) and Cowbird, Molothrus ater (Lustick, 1970).

The lines relating oxygen consumption to ambient temperature (Figs. 5 to 8) below the lower critical temperature follow the biological linear approximation to overall heat transfer (Bakken and Gates, 1974) as predicted by Scholander, et al. (1950). This phenomenon, whereby smaller mammals and birds increase metabolism with falling ambient
temperature, is well-documented in the literature. At 0°C both chickadees have a mean standard metabolic rate of about 11.5 ccO_2/g/hr. For a passerine this metabolism is fairly high compared to other species. Standard metabolic rate for the Cowbird (33 g) at 5°C is approximately 4.5 ccO_2/g/hr (Lustick, 1970); the Red Crossbill (Loxia curvirostra), a 30 g bird, uses 4.5 ccO_2/g/hr at 0°C (Dawson and Tordoff, 1964); and the House Sparrow (25 g) at 0°C has a metabolic rate of 6.5 ccO_2/g/hr (Hudson and Kimzey, 1966). Since a higher metabolism allows a small bird to be more active at lower temperatures, the high metabolic rate for chickadees appears to be an important advantage. Another adaptive feature of a high metabolism is that it allows a bird to more readily establish itself as a resident species at low temperatures, rather than migrate (Kendeigh and Blem, 1974). Since both chickadees are fairly resident in their range, resident status would seem to favor a high metabolism.

At night the Carolina had a significantly lower metabolic rate below thermoneutrality than the Black-capped. The thermoregulatory ability to maintain a lower metabolic rate indicates the Carolina is also lowering its body temperature and suggests that the Carolina may not be necessarily restricted to its northern boundaries on the basis of energetics (regulation of body temperature). If the Carolina Chickadee can lower its body temperature in
response to decreasing ambient temperature, and thus increase its tolerance to cold, the species could conceivably increase its range as several other passerines have been known to do, assuming that other environmental factors and species competition would allow this to happen. The lower metabolic rate in the Carolina may have occurred because the ambient temperature was comparatively lower for it, when contrasted to the Black-capped which probably experiences lower environmental temperatures than the Carolina naturally does. The Black-capped is also slightly larger and may not have been as stressed as the Carolina at lower temperatures. Data on body temperature (Fig. 12) show the Carolina drops its body temperature below that of the Black-capped, especially at 0°C.

The studies on oxygen consumption over a 24-hour period at 25°C demonstrate the similarity of the two species in respiratory metabolism in the thermal neutral zone. At 10°C (Fig. 10), the Carolina maintained a lower metabolic rate over the entire period, reflecting its lower body temperature (Figs. 11 and 12). A lower nocturnal metabolism was also shown for fasted birds (cf. Figs. 7 and 8). In his study on the Abert and Brown Towhees, Dawson (1954) measured body temperature over a 24-hour period at 5°C. His results indicated a lower metabolism for the Brown Towhee, also the smaller and the more southern of the two species.
The data from Figs. 9 and 10 indicate the birds reached a postabsorptive state, i.e. the point of minimum oxygen consumption, within one and a half to two hours. One can also note from Tables 4 and 5 that the birds, when allowed to maintain a normal dark period, had a lower metabolic rate than was obtained for birds tested in a darkened chamber either during the day or night.

**Body Temperature**

Passerines are estimated to have a body temperature falling within the range 39.2° to 43.8°C (Dawson and Hudson, 1970) for the active phase of their daily cycle. Regardless of ambient temperature the towhees (Dawson, 1954), Gray Jay, *Perisoreus canadensis* (Veghte, 1964), and Cowbird (Lustick, 1970) appear to fall in or near this range. In thermoneutrality, chickadees were also found to fall within this range. Daytime body temperature ranged from 39° to 42°C, while nighttime body temperature varied between 38° and 41°C. Below thermoneutrality with an increase in metabolic rate, chickadees gradually decreased body temperature with decreasing ambient temperature indicating heat production did not equal heat loss. This hypothermia resulted in an approximate decline of four degrees in body temperature from the lower critical ambient temperature to 0°C, except for the Carolina Chickadee at night which dropped its temperature 7.6°C. Steen (1958) reported
hypothermia for six small species of birds, including the Great Tit. Budd (1972) also found evidence of hypothermia in Black-caps and reported a difference of 10° to 12°C between diurnal and nocturnal body temperatures. Assuming that Budd calculated 42°C as diurnal body temperature and 30°C as nocturnal, I found the same temperature difference in the Carolina Chickadee (41.5°C vs. 30.5°C). Since the birds had to be handled when body temperature was taken, it might be even lower under normal conditions.

One would expect that a ten-gram animal would have some adaptive mechanism for survival in a situation where sub-freezing temperatures create a physiological stress and food-limiting environment. The results presented imply that chickadees utilize their ability to decrease body temperature to reduce energy demands at lower winter temperatures. A larger surface area to volume ratio, which is characteristic of small animals such as chickadees, means a greater heat loss compared to larger animals. The lowering of body temperature decreases the gradient between body and ambient temperatures, and as a consequence results in less heat loss for the animal. For Black-capped Chickadees, dropping the body temperature at night at 0°C results in a 27% decrease in oxygen consumption compared to diurnal values; for Carolina Chickadees, it results in a 32% decrease. The energy saving from a low body temperature is appreciable and represents an important adaptive
mechanism to low air temperatures for both chickadee species.

There is a question regarding the chickadees' use of nest holes as microhabitats in winter as some life histories suggest (Forbush and May, 1939). Odum (1942) mentions the occasional use of woodpecker holes or natural cavities, which confirms the observations made in the field and in the laboratory during the course of this study. Brewer (1961) does not mention the use of nest holes at all in the case of the Carolina. From the hypothermic response exhibited by chickadees, the use of nest holes would not seem to be important as a mechanism for conserving energy in cold weather.

At temperatures above thermoneutrality, body temperature apparently increases with increasing metabolic rate and is maintained slightly above air temperature. Since hyperthermia increases the temperature gradient into an animal, the requirement for evaporative cooling is also reduced. Losing water by evaporative cooling is accomplished by panting in birds and requires that energy be expended. Allowing the body temperature to rise with increasing air temperature, permits the passive heat flow from the bird to the environment, thereby constituting another energy-saving device. Other species of passerines have been noted to utilize hyperthermia (Dawson, 1954; Hudson and Kimzey, 1966; Lustick, 1970), which agrees with
the findings of Lasiewski et al. (1966) that hyperthermia is used to a conspicuously greater degree in smaller passerines (<50 g) compared to larger birds. Chickadees were not subjected to temperatures higher than 40°C because of increased mortality which resulted at 40°C. Mortality probably resulted from other stresses as well. Observations at temperatures higher than 40°C would be useful in the further assessment of chickadee hyperthermia.

Thermal Conductance

Thermal conductance has been characterized as the "umbrella" of factors that affect the heat flow between the animal and its environment. Within thermoneutrality, thermal conductance increases with increasing ambient temperature, while below the thermal neutral zone, thermal conductance remains fairly constant as heat production increases with decreasing environmental temperature. By comparing the shape of the metabolic curves (Figs. 5 to 8) with those of thermal conductance (Figs. 17 to 20), one can observe this relationship for the two species of chickadees. Lasiewski, Weathers, and Bernstein (1967), using data from 40 avian species, determined an equation for predicting conductance below thermoneutrality on the basis of body weight. The equation is as follows:

\[ \log C = \log 0.848 - 0.508 \log W \]

where \( C \) is thermal conductance in \( \text{cc} \) \( \text{O}_2 \)/g/hr/C, and \( W \) is
body weight in grams. Mean thermal conductance for both species of chickadees was 0.32 ccO₂/g/hr/°C, during the day and about 0.265 ccO₂/g/hr/°C at night. These values approximate the prediction for a ten-gram bird which is 0.30 ccO₂/g/hr/°C.

West (1965) and others (see Dawson and Hudson, 1970) have demonstrated that small, wild birds employ shivering thermogenesis at environmental temperatures below thermo-neutrality. The works by Hart (1962) and West (1965) suggest that shivering in birds is a primary mechanism for thermoregulating in order to maintain a constant body temperature. One would expect this to be true of chickadees also, but the data on hypothermia seem to indicate that lowering of body temperature is equally, if not more, important in adapting to lower ambient temperatures. Budd (1972) has suggested that the lack of shivering activity with passive decline of core temperature is the mechanism on which chickadee hypothermy is based.

Other factors, such as decreased evaporative water loss (Figs. 15 and 16), behavior, and feather adjustment appear to be important to chickadees in regulating body temperature. Veghte and Herreid (1965) illustrate changes in feather arrangement at decreasing ambient temperature in the Black-capped Chickadee. Radiometric determination by Veghte and Herreid show the head to be one of the warmest of the body regions. Heat loss apparently is reduced
in small birds by tucking the head beneath the back feathers. A roosting chickadee appears as little more than a ball of feathers with an extreme degree of piloerection. (Observations from the present study also showed that a chickadee will select a roosting site close to a stump if offered, in a depression on top of a stump, and possibly a hole.)

Veghte and Herreid (1965) show a general relationship to exist between the size of the bird and the average surface temperature of the feathers. As ambient temperature decreased, the feather surface temperature of a large bird, the Common Raven (*Corvus corax*), decreased, while the bird itself maintained a high cloacal temperature. Feather surface temperature decreased in Black-capped Chickadees, but it did not approach ambient temperature as it did for the larger bird. Because of a relatively larger surface area, smaller birds must expend more energy to maintain a high core temperature. A hypothermic response would help alleviate this energy expenditure to adverse, decreasing environmental temperature.

**Evaporative Water Loss**

The generally accepted mode of heat loss in birds is evaporative cooling via the respiratory surface especially at high ambient temperatures. This is accomplished chiefly by panting and accounts for at least 50% of the heat loss in small birds at high air temperatures (e.g. 40°C to 45°C).
(Cade, 1964; Lasiewski et al., 1966). Other mechanisms that are involved in heat loss are cutaneous evaporation (Dawson and Hudson, 1970), radiation, convection, conduction, and hyperthermia.

Data for water loss in chickadees compares favorably with other small passerines at low air temperatures. Lustick (1970) found the heat loss to be approximately 20% for the Cowbird at 25°C. At the same temperature Black-capped Chickadees lost about 12% of heat produced by evaporative cooling. The Carolina Chickadee lost about 16% of its heat load by this method. In terms of water lost per day on a diurnal basis at 25°C this amounts to 1.21 grams for the Black-capped and 1.45 grams for the Carolina. The Zebra Finch (*Poephila castanotis*), a small desert bird weighing about 11.5 grams, was found to lose 3.30 (Calder, 1964) and 2.38 (Cade, Tobin, and Gold, 1965) grams of water per day. Crawford and Lasiewski (1968) have produced several equations by which evaporative water loss may be predicted on the basis of body weight at 25°C. Evaporative water loss in chickadees is in close agreement with the equation for all birds. The all bird equation is as follows:

\[
\log E = \log 0.432 - 0.585 \log W
\]

where \( E \) is evaporative water loss in g H\(_2\)O/day and \( W \) is body weight in grams.
When the chickadee data for evaporative water loss were calculated for higher air temperatures (35°C and 40°C), the birds were found to be losing less than 25% of the heat produced (Figs. 15 and 16). These results indicate the chickadee loses less water by evaporation than expected, and this contrasts with the results obtained by Cade et al. (1965) and Lustick (1970), who found desert finches and the Cowbird respectively could lose 100% of their heat load by evaporative water loss. Two reasons may be cited for the low figure for chickadees. First, chickadees may not have the capability of losing large amounts of heat by evaporative cooling. Increased mortality at 40°C seems to imply this may be true. To fully ascertain whether chickadees are incapable of losing greater heat loads by evaporation, these studies should be continued at the same temperature for a longer period of time and also at increased ambient temperatures.

Since results at 25°C are correct, one must assume the results at 40°C are also. Thus, chickadees may use alternative means of dissipating the larger heat loads encountered at high air temperatures. Lasiewski et al. (1966) note that increased levels of hyperthermia in smaller passerines, compared to larger birds, may be due to a combination of several factors: (1) a relatively higher non-hyperthermic body temperature in small birds and (2) the
Lasiewski et al. further examine a series of situations in which evaporative water loss and heat production are presented in different situations. In one such situation evaporative water loss is less than heat production, and the temperature of the bird comes to equilibrium slightly above ambient temperature through heat loss by a variety of means. Chickadees meet the above criteria considering their size and high metabolic rate. My studies on body temperature at 40°C have shown chickadees to undergo a moderate hyperthermia, increasing body temperature to about 42°C. This was also shown to occur when the birds were exposed to artificial solar radiation. Hyperthermia serves to increase the thermal gradient between the animal and its environment, resulting in a net increase of heat flow out of the bird. Hyperthermia and the resulting increase in radiation, convection, and conduction seem to be the important additional avenues for heat dissipation in the chickadee as indicated by the high dry heat flow at 40°C (Figs. 17 and 18).

Ad Libitum and Minimum Water Consumption

In captivity chickadees drink and bathe readily. In northern areas, eating snow and snow-bathing are common (Odum, 1943). Their diet is an omnivorous one, consisting of approximately 50% insects in winter and anywhere from
70 to 100% insects in the warmer seasons (Bent, 1946). Like other temperate species, chickadees are found near ample supplies of water. Results of ad libitum water consumption at 20°C show that the chickadee drinks water equivalent to 50% of its body weight in water each day. This value agrees with the prediction by Bartholomew and Cade (1963) for a ten-gram bird, which is based on the inverse relationship of body weight and water consumption. The same has been shown to be typical of many other temperate passerines, most of which are finches (Cardinal, Dark-eyed Junco, House Sparrow, etc.). Dawson (1954), Cade et al. (1965), Lustick (1970), and others have shown water consumption increases with increasing environmental temperature. Increased drinking is significant, especially for those species living in a xeric habitat. The Carolina Chickadee occurs in semi-arid areas of Okla. and Texas, and an analysis of its water requirements in this area would be of interest. The Verdin (Auriparus flaviceps), a parid which geographically overlaps with the Carolina here, is not known to drink (Taylor, 1971).

Chickadees can adapt to decreases in the supply of available water as indicated by the studies on minimum water. The minimum water consumed for Black-caps was about 2.3 ml or approximately 40% of the ad libitum value; minimum water for Carolinas was 2.8 ml, about 45% of the ad libitum amount. One Carolina was noted to require only 1.5 ml or
75% less than its *ad libitum* consumption. Comparative data on temperate passerines are lacking, as most studies on minimum water have concentrated on desert passerines. Lustick (1970) found minimum water consumption for the Cowbird to be 3.4% of its body weight per day; Poulson and Bartholomew (1962) found it to be 10% in the House Finch (*Carpodacus mexicanus*). The minimum water consumption for chickadees is approximately 25% of the body weight per day.

Bartholomew and Cade (1956) and Lustick (1970) found that their birds returned to the normal body weight after 24 hours rehydration. Chickadees did not attain their former weight until after 48 hours rehydration, which is some indication that living in a dry climate would present a problem for these species.

**Oxygen Consumption and Artificial Radiation**

Birds are known to reduce their energy expenditure in several ways under cold stress: postural adjustments, changes in feather arrangement, huddling, circulatory changes, and possible use of shelters. For some time environmental physiologists have speculated that solar radiation may also contribute to reducing metabolic rate. White-crowned Sparrows (*Zonotrichia leucophrys*), receiving artificial solar radiation at 7°C, have been known to decrease food intake compared to those which did not receive it (Morton, 1966). Hamilton and Hepner (1967) have shown that
Zebra Finches, when dyed black, can reduce their metabolic rate when exposed to artificial radiation at low air temperatures ($10^\circ C$). Basking Cowbirds at $10^\circ C$ reduce their metabolism by 26% while maintaining body temperature, which results in a considerable energy savings compared to birds not receiving radiation (Lustick, 1969). Considering the winter temperatures to which northern chickadees are exposed their plumage, and the above results, one could ask whether solar radiation might be useful in decreasing the metabolic load of these birds at low environmental temperatures.

At $5^\circ C$ chickadees reduced their oxygen consumption slightly (10%), but not significantly, when exposed to artificial radiation. That no great difference in metabolic rate occurred between chickadees exposed to artificial radiation and those not exposed is not entirely surprising. Chickadees are woodland species and do not seem to spend a great amount of time basking or foraging in open areas. They are restricted mostly to mixed deciduous or heavy coniferous habitats. The normal activity pattern for chickadees consists mostly of short, quick flights, the birds moving constantly as they forage. The activity studies made in this research corroborate that a change in radiation does not affect this behavior.

Although hyperthermia was statistically indistinguishable between radiated and non-radiated birds, the two degree
hyperthermic response in birds exposed to radiant energy indicates the birds were absorbing radiant energy. With solar radiation the surface temperature of the bird rises, thus decreasing the gradient from the core to the surface of the animal. As a consequence, the heat flow (heat loss) from the animal is reduced, resulting in a savings of energy. I could find no other comparable data on passerines where solar radiation produced a hyperthermia under cold stress. Neal and Lustick (1973) found a $1.2^\circ$C increase in the body temperature of the Eastern Chipmunk (Tamias striatus) when exposed to solar radiation at $10^\circ$C. In the chipmunk the increase was accompanied also by a significant ($P<0.05$) downward shift in metabolism.

Ohmart and Lasiewski (1971) have found the Roadrunner (Geococcyx californianus) undergoes a nocturnal hypothermia below $10^\circ$C. Exposure to artificial radiation allows the hypothermic Roadrunner to increase body temperature while maintaining a low metabolism. Apparently solar radiation causes a decrease in metabolism and an increase in body temperature in chickadees, resulting in a slight energy-saving mechanism in regard to low environmental temperatures. Behavior reflects physiology, and this conclusion is supported in the field studies by Lawrence (1958). Lawrence observed on cold, clear mornings, Black-capped Chickadees perch high in a tree or in a sheltered location,
basking in the sun before beginning to feed. As the sun rises, chickadees steadily accelerate their feeding activity. Lawrence also found as environmental temperature declined, feeding tempo increased. This implies at higher environmental temperatures, feeding activity may be reduced. From these observations and my results, I suggest that after a night in hypothermia, at low ambient temperatures, chickadees utilize solar radiation to increase body temperature in the morning. Activity level increases, and energy reserves are built up during periods of feeding activity. With higher air temperature, metabolic rate and feeding may subside, the birds maintaining a high body temperature (e.g. 39°C to 40°C) which results in reduced energy demands. When ambient temperature decreases, feeding activity may be stimulated again.

In addition, Lawrence noted feeding changes occurred without any perceptible indication that weather changes were about to occur. Based on these behavioral observations in regard to weather changes, Lawrence speculated some sort of internal regulating mechanism might exist which enables chickadees to detect these weather changes prior to actual occurrence. Considering that chickadees are able to alter body temperature with apparent ease either upwards or downwards, this detection device must also enable the chickadee to readily thermoregulate in
response to temperature and thus effect appropriate behavior as well.

A Conclusion

In undertaking the research described, an initial question was, if two birds are presently described as distinct species, then should not the energetics of the two species reflect their separateness. Although intensely similar in many aspects, the Black-capped Chickadee and Carolina Chickadee differ principally in ranges and could therefore be expected to manifest this physiologically. With respect to temperature range, the Black-capped Chickadee is restricted to a different range from that of the more southern Carolina Chickadee. Each species, therefore, experiences a different set of temperature extremes. Under a set of controlled temperatures, including stresses imposed by the extremes, a physiological variation could be anticipated. Two unique species, two unique environments should result in two unique physiological responses to changes in those thermal environments.

Physiologically, however, the results of this research on two Ohio populations do not show any significant variation in terms of energetics. Determining and comparing the energetics of specimens from the extremes of the ranges would be valuable to further document similarity or variability. This is beyond the scope of the present research,
but the results presented support Brewer's claim (1963) of recent evolutionary divergence. Based on thermoregulatory ability, one can even assert no species difference and argue that *Parus atricapillus* and *P. carolinensis* are variations of the same species. *Atricapillus* and *carolinensis* would then be subspecies with slight differences in behavior and very slight differences in morphology. General changes in morphometric features (e.g. wing chord, weight), in fact, define the cline concept of increasing body size with increasing latitude to an appreciable degree. Variations in chickadees regarding clines do exist as pointed out in a previous section.

The genetic similarity of the two species is apparent according to other investigators. Hybridization appears to be well-documented where ranges of the species are contiguous (Brewer, 1963; Rising, 1968; Johnston, 1971). Studies by Brewer and Rising report on viable hybrids and suggest mixed breeding pairs occur. Johnston cites evidence of hybrids, displaying a continuum of intermediate morphometric and song characteristics, and strongly suggests the maintenance of several intermediate generations. The above evidence furthers the argument for conspecificity of the two chickadees, as the results of the present study show. Variations in physiological responses were found to exist. But climatic differences, especially in regard to
temperature, generally did not produce significant differences in the energetics of these two species of chickadees. The clear implication is that physiologically Parus atricapillus and P. carolinensis are the same species.
SUMMARY

1. The energetics of the Black-capped Chickadee and Carolina Chickadee were measured over the temperature range of 0° to 40°C. Standard metabolism was determined as the amount of oxygen consumed per gram per hour. Measurements of weight, body temperature, evaporative water loss, thermal conductance, water requirements, and standard metabolism under conditions of artificial solar radiation were also made and compared.

2. The zone of thermoneutrality was found to extend from 25° to 35°C for both species. Within thermoneutrality the diurnal standard metabolism was 4.7 ccO₂/g/hr for the Black-capped Chickadee and 4.5 ccO₂/g/hr for the Carolina Chickadee. Nocturnal metabolic rates were 3.2 and 4.1 ccO₂/g/hr for the Black-capped Chickadee and Carolina Chickadee respectively. Below thermoneutrality, metabolic rate followed the linear approximation to overall heat transfer. Statistically, no difference was found between the metabolic curves for the two species.

3. Non-fasting metabolism was measured over a 24-hour period at 25° and 10°C. Both species displayed a similar metabolic rhythm. The Carolina Chickadee maintained a
slightly lower metabolism at $10^\circ$C.

4. Except for slight variations, no distinguishable difference in energetics exists between the Black-capped Chickadee and Carolina Chickadee. A weight difference between the two species was apparent. Fasted mean weight for the Black-capped was 11.1 g; fasted mean weight for the Carolina was about 9.9 g.

5. Below thermoneutrality, chickadees undergo hypothermia, decreasing body temperature as ambient temperature decreases. Hypothermia may result in a $10^\circ$ to $12^\circ$ decrease in body temperature for both species at $0^\circ$C. At night with low environmental temperatures, decreased body temperature means a decrease in metabolism, which represents an adaptive mechanism in energy conservation. Nocturnal hypothermia represents an energy savings of 27% in terms of oxygen consumption for the Black-capped Chickadee and an energy savings of 32% for the Carolina Chickadee at $0^\circ$C. Above thermoneutrality, chickadees undergo a slight hyperthermia.

6. Thermal conductance remained constant below thermoneutrality and increased within the thermal neutral zone as ambient temperature increased. Regulation of body temperature and factors that are important in contributing to decreasing thermal conductance at low air temperatures are discussed.

7. Chickadees do not appear to have the capability of
losing large amounts of heat by evaporative cooling at high air temperatures (e.g. 40°C). Dry heat flow, calculated from thermal conductance, indicated a large amount of heat is eliminated by means other than evaporative cooling at high temperatures.

8. Ad libitum water consumption was determined to be 5.6 ml for the Black-capped Chickadee and 5.9 ml for the Carolina Chickadee. Minimum water consumption was 2.3 ml and 2.8 ml.

9. When exposed to artificial solar radiation at 5°C, chickadees increased body temperature and decreased metabolic rate slightly. Field studies and this research indicate chickadees utilize solar radiation to increase body temperature on cold mornings after a period of nocturnal hypothermia.

10. Studies have shown the Black-capped Chickadee and Carolina Chickadee are very similar in aspects of morphology, ecology, and behavior. Other research reports that hybridization occurs between the two species and cites evidence of reproducing hybrids. The present research further illustrates the close phylogenetic relationship of the chickadees and provides support for a single-species concept on the basis of energetics.
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