

SEASONAL ACCLIMATIZATION OF THERMOREGULATION IN THE BLACK-CAPPED CHICKADEE¹

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Abstract. Black-capped Chickadees (*Parus atricapillus*) show behavioral adaptations (food caching, cavity roosting) and can undergo regulated bouts of nocturnal hypothermia, both of which reduce costs associated with wintering in temperate latitudes. These adjustments could reduce the need for the seasonal metabolic adjustments found in other small passerines that must deal with severe winter cold. We have examined this possibility by determining the extent of seasonal variation evident in chickadees concerning standard metabolic rate, metabolic response to temperature, cold resistance, and maximal thermogenic capacity ($\dot{V}O_2^{\text{sum}}$). Regression equations relating metabolism to air temperature below thermoneutrality did not differ significantly in either slope or Y-intercept between summer and winter, and neither did minimum thermal conductance for normothermic birds vary seasonally. Seasonal constancy in these parameters demonstrates the minor role that seasonal changes in insulation play in acclimatization in chickadees. However, winter birds tolerated cold stress far better than summer birds. This improved cold tolerance was associated with a significant increase in $\dot{V}O_2^{\text{sum}}$ (36%) in winter relative to summer. Standard metabolic rates (SMR) were also significantly increased in winter birds compared to summer birds. Thus, Black-capped Chickadees show seasonal metabolic acclimatization similar to, or greater than, other temperate wintering passerines in addition to behavioral adaptations and nocturnal hypothermia.

Key words: Black-capped Chickadee; *Parus atricapillus*; cold tolerance; maximal thermogenic capacity; standard metabolic rate; thermoregulation.

INTRODUCTION

Overwintering of small birds in cold temperate regions requires prolonged expenditures of energy in regulatory thermogenesis. In addition, foraging time is decreased in winter due to shorter days and can be further restricted by heavy snow or ice cover. Coincident with these seasonal changes, cold temperate-wintering passerines undergo seasonal acclimatization which facilitates maintenance of thermoregulatory homeostasis. Winter-acclimatized birds are generally much better at tolerating cold than summer birds (Hart 1962, Barnett 1970, Pohl and West 1973, Dawson and Carey 1976, Dawson et al. 1983, Dawson and Smith 1986, Swanson 1990).

Seasonal variation in maximal thermogenic capacity ($\dot{V}O_2^{\text{sum}}$) in small birds has received some attention (Hart 1962, Dawson et al. 1983, Dawson and Smith 1986, Marsh and Dawson 1989, Swanson 1990). Historically, documenting sea-

sonal changes in $\dot{V}O_2^{\text{sum}}$ was difficult due to problems generating experimental temperatures low enough to elicit maximum metabolism. Highly conductive helium-oxygen gas mixtures (helox) facilitate heat loss without impairing oxygen uptake and thereby allow peak rates of cold-induced thermogenesis at relatively moderate temperatures (Rosenmann and Morrison 1974). Helox gas mixtures have been used to show winter increases in cold-induced thermogenesis in several small mammals (Feist and Rosenmann 1975, Rosenmann et al. 1975, Wickler 1980, Sparti 1992, Hinds and Rice-Warner 1992). This method has also been used to document increased $\dot{V}O_2^{\text{sum}}$ associated with improved cold tolerance in winter-acclimatized American Goldfinches (*Carduelis tristis*; Dawson and Smith 1986) and Dark-eyed Juncos (*Junco hyemalis*; Swanson 1990) relative to summer birds.

Adjustments in insulation assist some passerines in winter improvement of cold tolerance. However, metabolic adjustments, associated with enhanced shivering endurance, in winter are primarily responsible for improved cold tolerance (Dawson and Carey 1976, Swanson 1991). These metabolic adjustments allow maximal thermo-

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genic capacity ($\dot{V}O_2^{\text{sum}}$) in winter-acclimatized passerine birds to exceed summer $\dot{V}O_2^{\text{sum}}$ by as much as 1.43 times (Marsh and Dawson 1989).

The Black-capped Chickadee (*Parus atricapillus*) is a small, largely nonmigratory passerine bird that occupies regions with relatively severe winter climates (Taverner 1949, Kron 1975, Kessel 1976, Desrochers and Hannon 1989). Black-capped Chickadees show behavioral adaptations such as food caching and cavity roosting (Odum 1942, Bent 1946), and can undergo regulated bouts of nocturnal hypothermia (Chaplin 1976) that reduce costs associated with temperate wintering. Since energetic costs of overwintering can be reduced by behavioral adaptations and nocturnal hypothermia, metabolic acclimatization to winter conditions might not be as marked in chickadees as in birds without these adaptations. Therefore, we studied seasonal variation in standard metabolic rate, metabolic response to temperature, cold hardiness, and maximal thermogenic capacity in Black-capped Chickadees from southeastern South Dakota to determine if behavioral adaptations and regulated hypothermia reduce seasonal metabolic adjustments in these birds relative to other temperate-wintering passerines.

METHODS AND MATERIALS

BIRDS

Black-capped Chickadees were captured in summer and winter by mist net before 11:00 hr near Vermillion, Clay County, South Dakota in 1991 and 1992. Body mass to the nearest 0.1 g was determined immediately upon capture with a Pesola spring balance (0–50 g with 0.5 g gradations). Accuracy to 0.1 g was validated by measurement against a Sartorius (Model 3704) balance accurate to 0.01 g. Upon capture, wing length, tarsus length, and tail length were measured, and visible fat was scored using a scale of 0–5 (Helms and Drury 1960). Birds were transported to the laboratory by 12:00 hr and caged at 20–25°C. While caged, birds were provided free access to food (wild bird seed and *Tenebrio* larvae) and water. All tests were conducted on the day of capture. Chickadees tested from 8 May to 31 August were designated “summer birds,” and those tested from 22 November to 29 February were designated “winter birds.” We were unable to distinguish sex in winter chickadees as methods other than brood patch and cloacal protuberance did

not allow sex discrimination (Cooper, unpubl. data). Consequently, birds were tested without regard to sex. Furthermore, Rising and Hudson (1974) found no differences in metabolism between male and female Black-capped Chickadees.

HELOX COLD STRESS

Cold stress tests were conducted using a gas mixture of approximately 79% helium and 21% oxygen. Temperatures for cold stress tests were 6°C, 4°C, and 3°C in summer, and –6°C, –9°C, and –12°C in winter. The lower temperatures at each season caused a majority of birds to become hypothermic. Previous studies documenting $\dot{V}O_2^{\text{sum}}$ in passerines indicate that helox temperatures resulting in hypothermia in a majority of individuals before 60 min elicit maximal thermogenesis and colder helox temperatures cause these birds to become rapidly hypothermic with depressed metabolic rates (Dawson and Smith 1986, Swanson 1990, Swanson 1993). This implies that the temperatures used in this study produced maximal thermogenesis, so lower temperatures were not employed. Individual chickadees were exposed to a single temperature within the series for 60 min, or until they became hypothermic (indicated by a steady decline in $\dot{V}O_2$ over several minutes). At the end of each test, birds were promptly removed from the chamber and cloacal temperature ($\pm 0.1^\circ\text{C}$) was recorded with a Cole-Parmer thermocouple thermometer (Model 8500-40) previously calibrated to a thermometer traceable to the U.S. Bureau of Standards and 20-gauge copper-constantan thermocouple. The thermocouple was inserted into the cloaca to a depth (approx. 10–12 mm) where further insertion did not alter the temperature reading. Birds with a cloacal temperature $> 37^\circ\text{C}$ were considered normothermic.

MAXIMAL OXYGEN CONSUMPTION MEASUREMENT

After at least 2 hr access to food, birds were placed in the metabolism chamber and gas flow into the chamber was initiated. Metabolic chambers were 3.8 liter paint cans filled approximately half-full with solid paraffin with the inner surface painted black. Chambers were equipped with a perch. The chamber was flushed with helox for 5 min ($1,000\text{--}1,020\text{ ml min}^{-1}$) prior to lowering the chamber into a water/ethylene glycol bath capable of regulating chamber temperature to

$\pm 0.5^{\circ}\text{C}$ (Swanson 1990). Chamber temperature was monitored continuously by a Cole-Parmer thermocouple thermometer (Model 8500-40). Chamber temperature was recorded every 60 sec along with excurrent oxygen measurements. Flow rates of dry, CO_2 -free gas through the metabolic chamber were maintained at 1,000–1,020 ml/min with a Cole-Parmer precision rotameter (Model FM082-03ST) calibrated to $\pm 1\%$ accuracy (Swanson 1990) and positioned upstream from the metabolic chamber. These rates yielded changes in oxygen content between influx and efflux gas of 0.3% to 0.6%, and maintained oxygen content of efflux gas above 20.3%.

We measured the rate of oxygen consumption (\dot{V}_{O_2}) during helox cold stress using open-circuit respirometry. The fractional concentration of oxygen in the respiratory gas during cold stress was measured with an Ametek Model S-3A oxygen analyzer. Measurements of dry, CO_2 -free efflux gas were recorded every 60 sec on a computer using Datacan 4.0 (Sable Systems) data collection software. Oxygen-consumption values were calculated as instantaneous rates (Bartholomew et al. 1981). The effective volume of the metabolic chamber was calculated according to the method of Bartholomew et al. (1981) and was 2,354 ml in the absence of a bird. The first ten minutes of \dot{V}_{O_2} measurements were omitted from calculations. We analyzed $\dot{V}_{\text{O}_2^{\text{sum}}}$ data according to Dawson and Smith (1986) by averaging instantaneous \dot{V}_{O_2} measurements over consecutive 10 min intervals. The highest 10 min mean \dot{V}_{O_2} was considered $\dot{V}_{\text{O}_2^{\text{sum}}}$ at the test temperature. Tests were conducted from 11:00 to 17:00 hr in summer and from 12:00 to 18:30 hr in winter.

STANDARD METABOLIC RATE AND METABOLIC RESPONSE TO TEMPERATURE

Procedures utilized to measure standard metabolic rate (SMR) and metabolic response to temperature (MRT) were similar to those for $\dot{V}_{\text{O}_2^{\text{sum}}}$ except air was used rather than helox. SMR and MRT were measured from 21:00 hr to 02:00 hr in summer and from 17:00 hr to 06:00 hr in winter. Chickadees were fasted for at least five hours before testing to insure post-absorptive conditions. Flow rates of dry, CO_2 -free air were maintained at 280–300 ml min^{-1} for both SMR and MRT. For SMR, chamber temperature was maintained at $30 \pm 0.5^{\circ}\text{C}$ which is within the thermal neutral zone for the chickadee (Chaplin 1974). For MRT, birds were exposed to tem-

peratures ranging from 17.0°C to -8.5°C . Individual birds were exposed to only a single temperature within this range for 60 min, except that in summer one bird was exposed to two temperatures and one bird was exposed to three temperatures with 15 min equilibration periods between temperatures. No differences in metabolic rate were apparent between the two birds tested at multiple temperatures and those measured at a single temperature. Following submersion of the metabolic chamber into the water/ethylene glycol bath for an equilibration period of at least 1 hr, metabolic rates were determined as the mean \dot{V}_{O_2} over a 60-min period. Oxygen consumption was calculated as steady state \dot{V}_{O_2} (Depocas and Hart 1957, Hill 1972, Eq. 2). All values for \dot{V}_{O_2} were corrected to STP.

STATISTICS

All values are presented as means \pm SD. Seasonal comparisons of SMR, $\dot{V}_{\text{O}_2^{\text{sum}}}$, body mass, and visible fat were by Student's *t*-test as variances were not significantly different (*F*-test for equality of variance). Birds that became hypothermic in <25 min had substantially lower $\dot{V}_{\text{O}_2^{\text{sum}}}$ than birds that remained normothermic for longer periods and were omitted from calculations of mean $\dot{V}_{\text{O}_2^{\text{sum}}}$. The effect of ambient temperature (T_a) in air and helox on body temperature (T_b) was analyzed by one-way analysis of variance (ANOVA) and if significant effects were detected, least squares regression. Comparison of slopes and intercepts of regression lines was by analysis of covariance. Statistical significance was accepted at $P < 0.05$.

RESULTS

BODY MASS AND FAT

Mean mass at capture for summer birds was 13.1 ± 0.7 g ($n = 50$) which did not vary significantly from winter birds (13.0 ± 0.9 g, $n = 60$). Differences in mass affect \dot{V}_{O_2} and in order to correct for differing masses, mass-specific ratios are often used. However, seasonal comparisons may be more effective using per bird \dot{V}_{O_2} (Dawson and Smith 1986, Swanson 1991). Thus, all values of \dot{V}_{O_2} are reported on both a total metabolism basis and a mass-specific basis. Mean furcular visible fat scores were 1.1 ± 0.6 ($n = 50$) in summer compared with 1.1 ± 0.6 ($n = 60$) in winter. Mean abdominal visible fat scores were 1.0 ± 0.4 ($n = 50$) in summer compared with

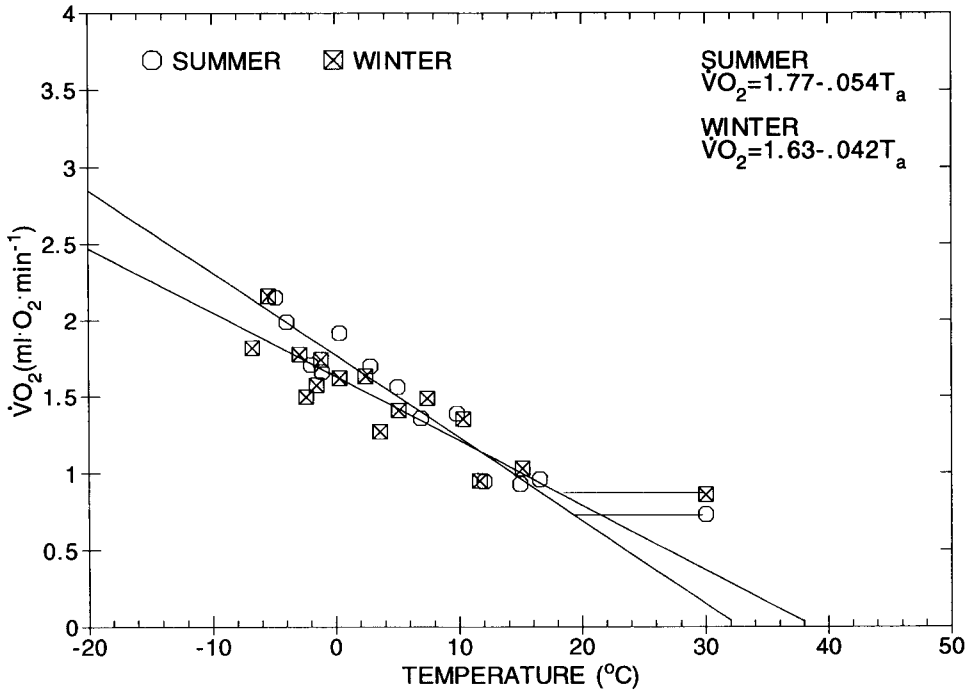


FIGURE 1. Relationship of total metabolism to ambient temperature in seasonally acclimatized Black-capped Chickadees. Equations given describe the regression line below thermoneutrality. The horizontal line represents SMR. On a mass-specific metabolism basis ($\text{ml O}_2 \text{ g}^{-1} \text{ hr}^{-1}$), equations below thermoneutrality were, Summer: $\dot{V}\text{O}_2 = 9.12 - 0.28T_a$ ($n = 12$, $R^2 = 0.87$, $P < 0.001$) and Winter: $\dot{V}\text{O}_2 = 7.88 - 0.24T_a$ ($n = 14$, $R^2 = 0.79$, $P < 0.001$). These mass-specific equations, like the per bird equations, did not differ significantly in either slope or intercept.

0.9 ± 0.5 in winter. There was no seasonal difference in visible fat scores.

METABOLIC RATE AND AMBIENT TEMPERATURE

SMR was $0.73 \pm 0.09 \text{ ml O}_2 \text{ min}^{-1}$ ($3.54 \pm 0.44 \text{ ml O}_2 \text{ g}^{-1} \text{ hr}^{-1}$, $n = 10$) in summer and $0.86 \pm 0.08 \text{ ml O}_2 \text{ min}^{-1}$ ($4.05 \pm 0.25 \text{ ml O}_2 \text{ g}^{-1} \text{ hr}^{-1}$, $n = 10$) in winter. SMR in winter was significantly elevated over summer SMR on both a total metabolism and a mass-specific basis ($P < 0.01$). Factorial increment in SMR in winter was 1.18 on a total metabolism basis and 1.14 on a mass-specific basis. SMR for summer chickadees exceeded allometrically predicted values by 8.9% whereas SMR for winter chickadees exceeded predicted values by 23.5% (Aschoff and Pohl 1970).

Below thermoneutrality, the relationship between total metabolism $\dot{V}\text{O}_2$ ($\text{ml O}_2 \text{ min}^{-1}$) and ambient temperature (Fig. 1) was best described by:

$$\text{Summer: } \dot{V}\text{O}_2 = 1.77 - 0.054T_a \\ (n = 12, \quad R^2 = 0.91, \quad P < 0.001) \quad (1)$$

$$\text{Winter: } \dot{V}\text{O}_2 = 1.63 - 0.042T_a \\ (n = 14, \quad R^2 = 0.76, \quad P < 0.001) \quad (2)$$

Slopes and intercepts did not vary significantly between seasons. Lower critical temperature (LCT) was calculated as the intersection of the regression line below thermoneutrality with a horizontal line through SMR. LCT was 19.3°C in summer on a total metabolism basis (19.9°C mass-specific basis) and was 18.3°C in winter on a total metabolism basis (16.0°C mass-specific basis) (Fig. 1).

For normothermic chickadees thermal conductance, calculated from individual values for $\dot{V}\text{O}_2$ below thermoneutrality, using the equation $C = \text{MR}/(T_b - T_a)$, (Scholander et al. 1950) was not significantly different between summer ($1.26 \pm 0.19 \text{ mW g}^{-1} \text{ }^\circ\text{C}^{-1}$, $n = 2$) and winter ($1.20 \pm 0.15 \text{ mW g}^{-1} \text{ }^\circ\text{C}^{-1}$, $n = 6$).

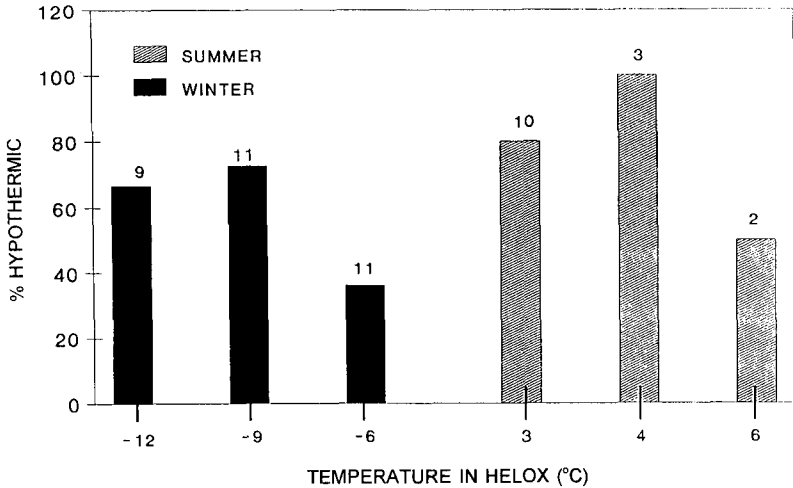


FIGURE 2. Cold tolerance in seasonally acclimatized chickadees over the 60-min test period. The numbers over the bars indicate sample size.

COLD TOLERANCE AND MAXIMAL OXYGEN CONSUMPTION

Winter-acclimatized chickadees tolerated colder temperatures in helox than their summer-acclimatized counterparts (Fig. 2). The average time it took for birds to become hypothermic was 45.8 min in summer and 39.8 min in winter. $\dot{V}O_2^{\text{sum}}$ was significantly greater in winter than in summer on both a total metabolism and a mass-specific basis (Table 1). In summer, $\dot{V}O_2^{\text{sum}}$ occurred from 3°C to 6°C and pooled $\dot{V}O_2^{\text{sum}}$ was $4.78 \pm 0.46 \text{ ml O}_2 \text{ min}^{-1}$, $n = 14$ ($23.23 \pm 1.79 \text{ ml O}_2 \text{ g}^{-1} \text{ hr}^{-1}$, $n = 14$). In winter, $\dot{V}O_2^{\text{sum}}$ occurred from -9°C to -12°C and was $6.49 \pm 0.55 \text{ ml O}_2 \text{ min}^{-1}$, $n = 29$ ($29.34 \pm 1.98 \text{ ml O}_2 \text{ g}^{-1} \text{ hr}^{-1}$, $n = 29$). Winter $\dot{V}O_2^{\text{sum}}$ represents a 36% increase over summer $\dot{V}O_2^{\text{sum}}$ (26% increase on a mass-specific basis). In summer, $\dot{V}O_2^{\text{sum}}$ was 6.7 times SMR on a total metabolism basis and 6.9 times on a mass-specific basis. In winter, $\dot{V}O_2^{\text{sum}}$ was elevated 7.9 times above SMR on a total metabolism basis and 7.5 times on a mass-specific basis.

We calculated thermal conductance in helox using a $T_b = 39.9^\circ\text{C}$ which was the pooled mean T_b of normothermic summer and winter birds under helox cold stress. For summer-acclimatized chickadees thermal conductance in helox was $3.61 \pm 0.31 \text{ mW g}^{-1} \text{ }^\circ\text{C}$ ($n = 14$) and for winter-acclimatized chickadees it was $3.38 \pm 0.21 \text{ mW g}^{-1} \text{ }^\circ\text{C}$ ($n = 29$). Thermal conductance in helox was significantly lower in winter-accli-

matized chickadees than in summer-acclimatized chickadees ($P < 0.01$), but this may simply reflect the ability of winter birds to withstand colder temperatures.

BODY TEMPERATURE

Mean T_b of normothermic birds after helox cold stress was $40.6 \pm 1.1^\circ\text{C}$ ($n = 2$) in summer and $39.1 \pm 1.4^\circ\text{C}$ ($n = 13$) in winter. For winter birds remaining normothermic throughout helox cold stress tests, T_b at the conclusion of cold stress was independent of T_a in helox. Mean T_b of normothermic birds after MRT in summer was $37.2 \pm 0.2^\circ\text{C}$ ($n = 2$) and $37.8 \pm 1.0^\circ\text{C}$ ($n = 7$) in winter. T_b was not dependent on T_a in air for normothermic MRT birds in winter. Lower T_b for normothermic MRT birds than for helox cold-stressed birds probably reflects measurement of MRT during the resting phase of the daily cycle, while $\dot{V}O_2^{\text{sum}}$ was measured during the active phase. In summer, at the completion of the MRT tests 77.8% of chickadees had become hypothermic. Hypothermia at the completion of MRT tests in winter occurred in 57.1% of individuals tested. Mean T_b of hypothermic birds after MRT in summer was $34.4 \pm 2.3^\circ\text{C}$ ($n = 6$) and $35.9 \pm 0.8^\circ\text{C}$ ($n = 8$) in winter.

DISCUSSION

Black-capped Chickadees in this study did not show seasonal variation in body mass or visible fat. This contrasts to a pattern of winter increases

in body mass and fat stores characteristic of many cold-temperate wintering passerines (King 1972, Dawson and Carey 1976, White and West 1977, Swanson 1991, Waite 1992). Chaplin (1974) documented winter increases in fat for Black-capped Chickadees from New York that were trapped in the afternoon. The chickadees in this study were captured in the morning and probably had not completely replenished fat stores depleted overnight. Consequently, seasonal variation in fat stores in these birds may have been underestimated. However, in several passerines, significant winter increases in fat also occur in morning-captured birds (Dawson and Carey 1976, Swanson 1991, Waite 1992). This suggests that chickadees fail to store fat in winter to the same degree as some other temperate-wintering passerines and that increases in fat stores are not a principal component of winter acclimatization in these birds. This finding agrees with the data of Rogers (1987) and Rogers and Smith (1993), who found that tree-feeding birds (including Black-capped Chickadees) maintain lower winter fat stores than ground-foraging birds.

Conductance below thermoneutrality was not significantly different between seasons for normothermic birds during MRT tests. In addition, LCT was only slightly higher for summer birds than for winter birds and the slope of the line relating metabolic rate to ambient temperature below thermoneutrality was not significantly different between seasons. Seasonal constancy in these parameters suggests little winter improvement of insulation and indicates that seasonal changes in insulation are not prominently involved in winter-acclimatization of the Black-capped Chickadee.

During MRT below thermoneutrality 77.8% of summer-acclimatized and 57.1% of winter-acclimatized Black-capped Chickadees became hypothermic. Chaplin (1974) estimated that Black-capped Chickadees can reduce their overnight energy expenditure by 32% by utilizing nocturnal hypothermia and maintaining T_b 10–12°C below daytime values. Nocturnal body temperatures from chickadees exposed to T_a below thermoneutrality in this study were often greater than 2–3°C below daytime values and demonstrate the possibility of regulated hypothermia. Such an adaptation may also confer significant energetic benefit on South Dakota chickadees.

Conductance in helox exceeded that in air by

TABLE 1. Maximal $\dot{V}O_2$ sustained over a 10-min period ($\bar{x} \pm SD$) at helox test temperatures in summer and winter chickadees. Body masses are means for the treatment group. Birds that became hypothermic in <25 min had substantially lower $\dot{V}O_2$ and were excluded from calculations.

Season/ temperature	n	Mass (g)	$\dot{V}O_2$ ml O_2 min ⁻¹	\bar{x} SMR
Summer				
6°C	2	11.9	4.82 ± 0.44	6.6
4°C	2	12.1	4.04 ± 0.32	5.5
3°C	10	12.5	4.92 ± 0.36	6.7
Winter				
-6°C	10	13.2	6.18 ± 0.47	7.2
-9°C	11	13.3	6.55 ± 0.59	7.6
-12°C	8	13.4	6.80 ± 0.42	7.9

2.86 times in summer and 2.82 times in winter. These values exceed increments in helox reported in House Sparrows (*Passer domesticus*; 1.72×, Koteja 1986), but are similar to values for Common Redpolls (*Carduelis flammea*; 2.6×, Rosenmann and Morrison 1974), American Goldfinches (2.7×, Dawson and Smith 1986), and Dark-eyed Juncos (3.0 times in winter and 3.1 times in summer, Swanson 1990). High factorial increments in conductance by helox indicate that heat loss in small birds is principally limited by insulation rather than by body tissues (e.g., subcutaneous fat) (Dawson and Smith 1986).

Black-capped Chickadees exhibit behavioral adaptations (food caching, cavity roosting), and undergo nocturnal hypothermia, which reduce overall energy requirements. However, these adjustments do not eliminate the requirement for elevating metabolic rate to increase heat production at low winter temperatures. For example, the mean daily temperature for Vermillion, South Dakota, is -8°C in January and 24°C in July (Environmental Data and Information Service, NOAA). We determined estimates of thermoregulatory costs (disregarding radiative and convective effects) by inserting mean daily temperatures for January and July into the equations relating metabolic rate to T_a below thermoneutrality, and solving for $\dot{V}O_2$ minus SMR. Estimated thermoregulatory costs were 35.8 kJ/day in January and 0 kJ/day in July. The estimated thermoregulatory cost of 35.8 kJ/day in winter represents 55% of the total daily energy expenditure reported by Karasov et al. (1992) for winter chickadees in Wisconsin. This marked in-

TABLE 2. Seasonal, geographic, and captivity status variation in standard metabolic rate in seasonally acclimatized Black-capped Chickadees.

Reference	Location	Summer SMR	Winter SMR	Status
		ml O ₂ g ⁻¹ hr ⁻¹		
Chaplin (1974)	New York	3.82	3.86	Captive
Rising and Hudson (1974)	New York	4.40	4.40	Captive
Grossman and West (1977)	Alaska	—	6.08	Captive
Present Study	South Dakota	3.54	4.05	Free-living

crease in thermoregulatory costs in winter suggests that acclimatization is directed toward elevated thermogenesis rather than improved insulation.

SMR varies seasonally in some passerines (Pohl and West 1973, Weathers and Caccamise 1978, Swanson 1991), but not in others (Dawson and Carey 1976, Dawson et al. 1985). For Black-capped Chickadees, SMR does not vary seasonally in outdoor captives, but is lower in winter than in summer for indoor captives (Chaplin 1974, Rising and Hudson 1974). SMR values in this study represent the only data for free-living chickadees and winter birds had significantly higher (18%) SMR than summer birds (Table 2). The seasonal variation in SMR in this study may reflect a metabolic difference between free-living and captive chickadees although our winter values are in relatively close agreement with Chaplin (1974) and Rising and Hudson (1974). Captivity can alter a number of parameters related to winter acclimatization including SMR (Warkentin and West 1990, but see Weathers et al. 1983), winter fattening and cold resistance (Dawson and Carey 1976, Dawson et al. 1983). In any event, the metabolic significance of seasonally changing SMR is not certain. Elevated SMR might be due to maintenance of the increased metabolic machinery needed for increased thermogenic capacity (Swanson 1991).

Maximal thermogenic capacity in winter-acclimatized Black-capped Chickadees exceeds summer $\dot{V}O_{2\text{sum}}$ by 1.36 times. This value exceeds those reported for House Finches (1.00 \times , Dawson et al. 1983), American Goldfinches (1.16 \times , Dawson and Smith 1986), and Dark-eyed Juncos (1.28 \times , Swanson 1990) and is only slightly below the highest value recorded for passerine birds of 1.43 times in House Sparrows (Hart 1962). This indicates marked seasonal metabolic adjustments in the Black-capped Chickadee.

Metabolic expansibility ($\dot{V}O_{2\text{sum}}/\text{SMR}$; Dawson and Carey 1976) for Black-capped Chicka-

dees was 6.7 in summer and 7.9 in winter on a total metabolism basis. The winter value is the greatest expansibility so far documented in passerine birds (Swanson 1990, Marsh and Dawson 1989) and approaches values for several small mammals (Feist and Rosenmann 1975, Rosenmann et al. 1975, Wickler 1980, Sparti 1992, and Hinds and Rice-Warner 1992). These metabolic expansibilities demonstrate that, relative to other passerines, chickadees are capable of elevating metabolism to a greater degree under cold stress.

We estimated air temperature equivalents for helox test temperatures by extrapolating the equations relating $\dot{V}O_2$ to T_a below thermoneutrality to $\dot{V}O_{2\text{sum}}$ and solving for T_a . Estimated air temperatures (disregarding radiative and convective effects) at $\dot{V}O_{2\text{sum}}$ were -65°C in summer and -148°C in winter. The actual air temperatures were probably not this low as thermal conductance changes with T_a below thermoneutrality, especially at very low temperatures. However, it is apparent that chickadees are capable of tolerating acute cold stress well below temperatures experienced under natural conditions. Daily mean minimum temperatures are 11°C in July and -10°C in January in Vermillion, South Dakota (Environmental Data and Information Service, NOAA, Fig. 3). Factors such as wind, humidity, and radiation might reduce the effective minimum air temperatures. However, chickadees are probably minimally affected by these factors during the night due to cavity roosting. Cavity roosting, which reduces radiative and convective heat loss, and may permit elevated air temperatures (Andreev 1980, Walsberg 1986) combined with nocturnal hypothermia accounted for a maximum of 50% energy expenditure savings in Carolina Chickadees (Mayer et al. 1982). However, during the day Black-capped Chickadees from South Dakota must at times face extremely cold effective minimum air temperatures while for-

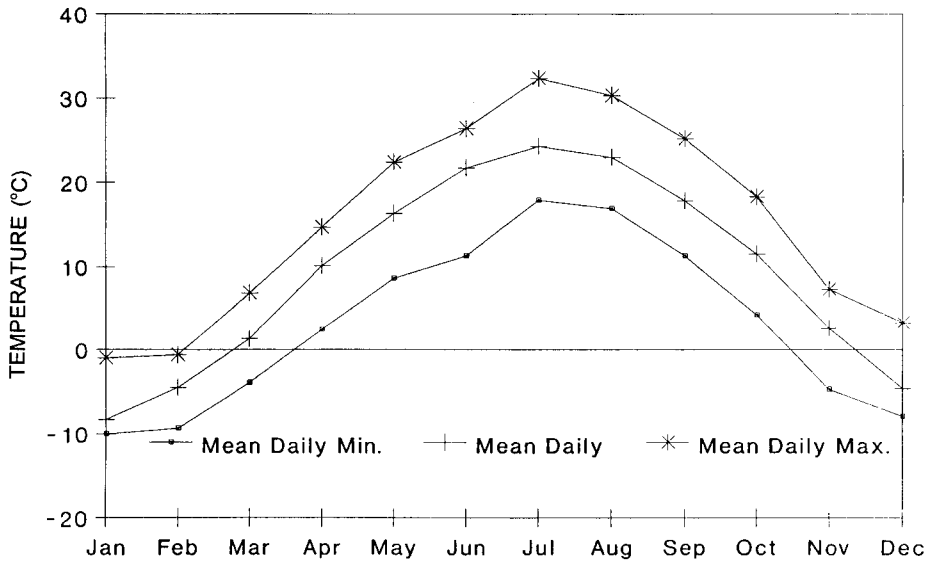


FIGURE 3. Annual temperature profile for Vermillion, SD. Daily energy expenditure for thermoregulation (0 kJ/day summer, 35.8 kJ/day winter) was determined using mean daily temperatures for July and January, respectively.

aging. Nevertheless, chickadees likely face little danger of hypothermia in natural environments given sufficient food.

Winter acclimatization in Black-capped Chickadees from southeastern South Dakota appears to be primarily a metabolic process in which SMR, maximal thermogenic capacity and cold tolerance are improved relative to summer. Metabolic acclimatization in Black-capped Chickadees is prominent in spite of behavioral adaptations and regulated hypothermia. The combined effects of these adaptations contribute to the overwintering success of Black-capped Chickadees in severe climates throughout much of their winter range.

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