Seasonal Metabolic Acclimatization in Mountain Chickadees and Juniper Titmice

Sheldon J. Cooper[*]

Department of Biology, Utah State University, Logan, Utah
84322-5305

ABSTRACT

Mountain chickadees and juniper titmice from northern Utah
were examined to determine metabolic and body-composition
characteristics associated with seasonal acclimatization. These
species use behavioral adaptations and nocturnal hypothermia,
which reduce energetic costs. These adjustments could reduce
the need for extensive metabolic adjustments typically found
in small passerines that overwinter in cold regions. In addition,
these species live at higher altitudes, which may also decrease
metabolic acclimatization found in birds. Winter birds tolerated
colder test temperatures than summer birds. This improved
cold tolerance was associated with an increase in maximal ther-
mogenic capacity or summit metabolism (M_{sum}). Winter M_{sum}
exceeded summer M_{sum} by 26.1% in chickadees and 16.2% in
titmice. Basal metabolic rates (BMR) were also significantly
higher in winter birds compared with summer birds. Pectoralis
wet muscle mass increased 33.3% in chickadees and 24.1% in
titmice in winter and paralleled the increased M_{sum} and BMR.
Dry mass of contour plumage increased in winter for both
species and was associated with decreased thermal conductance
in winter chickadees compared to summer chickadees. Chick-
adees and titmice show metabolic acclimatization similar to
other temperate species.

Introduction

For small birds that overwinter in cold-temperate regions, the
onset of winter creates energetically challenging conditions.
These conditions include low air temperatures and decreased
foraging time due to shorter days, which can be further re-
stricted by snow or ice cover. Small birds meet this energetic

[*] Present address: Department of Biology and Microbiology, University of
Wisconsin, Oshkosh, Wisconsin 54901-8640; e-mail: cooper@uwosh.edu.

challenge primarily through metabolic adjustments (reviews:
Dawson and Marsh 1989; Marsh and Dawson 1989*a*, 1989*b*;
Dawson and O'Connor 1996). These metabolic adjustments
generally include tolerance of colder temperatures in winter-
acclimatized birds relative to summer birds (Hart 1962; Barnett
1970; Pohl and West 1973), increased thermogenic endurance
in winter birds (Dawson and Carey 1976; Dawson et al. 1983;
Swanson 1990; O'Connor 1995), and increased summit me-
tabolism (M_{sum}) in winter birds (Hart 1962; Dawson and Smith
1986; Swanson 1990; Cooper and Swanson 1994; O'Connor
1995; Liknes and Swanson 1996).

The mountain chickadee (*Poecile gambeli*) and the juniper
titmouse (*Baeolophus griseus*) are small, largely nonmigratory
passerine birds that occupy regions of western North America.
The mountain chickadee's distributional range extends to
northern British Columbia (60°N), whereas the juniper tit-
mouse's range extends to portions of southern Oregon and
Idaho (44°N; Godfrey 1986; Cicero 1996). In addition, moun-
tain chickadees and juniper titmice live at relatively high alti-
tudes (~700–3,300 m; Bent 1946). Thus, both species inhabit
regions that have severe winter climates. Seasonal acclimati-
zation may be affected by high altitude. House finches from
Colorado have a different pattern of seasonal acclimatization
compared with Michigan house finches. Both Michigan and
Colorado house finches have seasonal fattening, increased cold
resistance, and increased catabolic capacity in winter. However,
Colorado finches do not have seasonal changes in M_{sum} as do
Michigan finches (Dawson et al. 1983; O'Connor 1996).
O'Connor (1996) states that these differences in seasonal ac-
climatization patterns may reflect either a direct or indirect
response to the different altitudes of the study sites.

Mountain chickadees and juniper titmice have behavioral
adaptations, including food caching and cavity roosting (Bent
1946), and use regulated bouts of nocturnal hypothermia (Coo-
per 1998), which reduce costs associated with temperate over-
wintering. For example, cavity roosting in mountain chickadees
and juniper titmice can reduce nocturnal energy costs from
25% to 38% in winter (Cooper 1999). Because behavioral ad-
aptations and nocturnal hypothermia reduce energetic costs,
chickadees and titmice may not have as marked seasonal met-
abolic acclimatization compared to birds without these adap-
tations. However, black-capped chickadees from South Dakota
show seasonal metabolic acclimatization similar to other tem-
perate wintering passerines in addition to behavioral adapta-
tions and nocturnal hypothermia (Cooper and Swanson 1994).

The aims of this study were to determine whether seasonal

acclimatization in mountain chickadees and juniper titmice is similar to that in black-capped chickadees and other species that exhibit marked seasonal metabolic adjustments or whether behavioral adaptations and regulated hypothermia reduce seasonal metabolic adjustments in these birds. I also wanted to determine whether M_{sum} changes seasonally in these high-altitude species. In addition, I wanted to determine whether changes in body composition are involved with seasonal metabolic acclimatization. Therefore, I studied seasonal variation in basal metabolic rate (BMR), cold tolerance, cold endurance, and maximal thermogenic capacity and body composition in mountain chickadees and juniper titmice from northern Utah.

Material and Methods

Birds

Mountain chickadees and juniper titmice were captured in summer and winter by mist net in 1994, 1995, and 1996. Mountain chickadees were captured in several locations within the Cache National Forest, Cache County, in northeastern Utah (41°52′N, 111°30′W; altitude 1,800–2,300 m). Juniper titmice were captured near Rosette, Box Elder County, in northwestern Utah (41°50′N, 113°25′W; altitude 1,700–1,900 m). These study sites are characterized by cold winter climates (Fig. 1).

Body mass to the nearest 0.1 g was measured on capture with an Ohaus model CT-1200 portable electronic balance. Visible fat depots in abdominal and furcular regions were also scored on capture, using a scale of 0–5 (Helms and Drury 1960). Following capture, birds were transported to the laboratory, where they were housed individually in 0.3-m^3 cages in a 3-m^3 temperature-controlled environmental chamber. The chamber temperature and photoperiod followed a cycle that approximated the season and study site to which the bird had been accustomed. While caged, birds were provided water, grit, and food (*Tenebrio* larvae and wild bird seed) ad lib. All birds maintained mass while in captivity. Daytime metabolic tests were performed on birds after allowing the birds a minimum of 2 h of feeding. Chickadees tested from June 1 to August 21 and titmice tested from May 11 to August 14 were designated "summer birds." Birds tested from November 25 to February 28 were designated "winter birds." For summer titmice, the M_{sum} of birds tested in May ($n = 5$) was not significantly different from June to August ($t = 0.64$, $P = 0.53$) and were therefore pooled with the June to August data.

Body Composition

Body composition was determined for a separate sample of wild birds captured before 0800 hours in summer and 0900 hours (MST) in winter. Birds were killed by cervical dislocation after body mass and fat scores were determined. Cervical dislocation was approved for use by the Utah State University Institutional Animal Care and Use Committee (protocol 602).
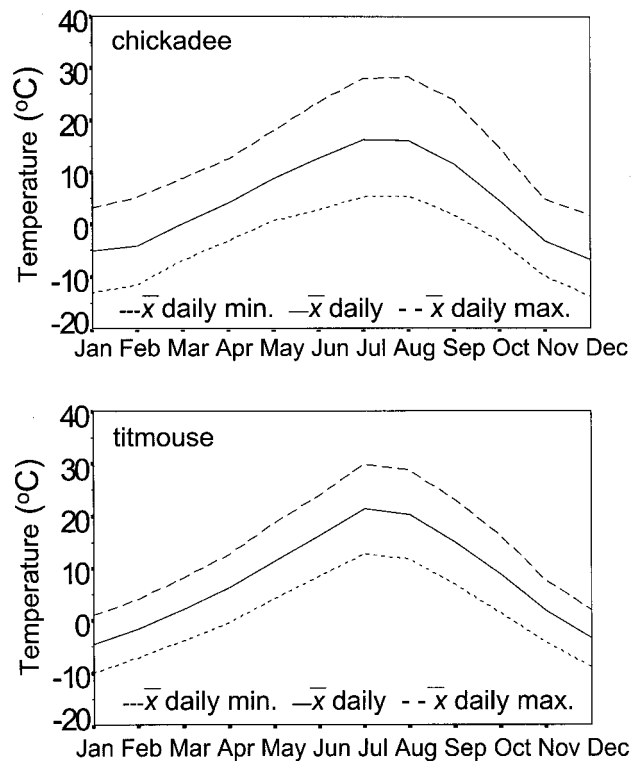

Figure 1. Annual temperature profiles for mountain chickadees and juniper titmice for study sites in northern Utah. Data are from the Utah Climate Center, Logan, 1989–1994.

The carcasses were then sealed in plastic bags, placed in an ice cooler in the field, and then stored in a freezer at −20°C on return to the laboratory. Contour plumage mass was determined by plucking and drying contour feathers in an open-ended vial at 50°–60°C. The right pectoralis muscle was dissected out of each carcass, and wet mass was measured. Carcass (including right pectoralis muscle), remiges, and rectrices were minced and dried at 50°–60°C to a constant mass. Neutral lipid was extracted from the dry carcass by Soxhlet extraction for 8 h in petroleum ether (Dobush et al. 1985). Following the ether extraction, the lean carcass was air dried for 6 h and then oven dried at 50°–60°C to constant mass. The difference between body mass at capture and dry mass equals the total body water. The difference between dry body mass and lean dry mass equals the extractable neutral lipid.

Helox Cold Stress

Cold-stress tests were conducted using a gas mixture of approximately 79% helium and 21% oxygen (helox). Helium is approximately four times more conductive than nitrogen. The high thermal conductivity of helox facilitates heat loss without impairing oxygen uptake and thereby allows maximal cold-

induced thermogenesis or summit metabolism (M_{sum}) at relatively moderate temperatures (Rosenmann and Morrison 1974). In addition, the effect of helox has been shown to be restricted to an increase in heat loss below the lower critical temperature in sugar gliders (Holloway and Geiser 2001). Cold-stress tests were conducted by placing individual birds into a metabolic chamber constructed from a 3.8-L paint can filled approximately one-third full with solid paraffin with the inner surface painted black to provide an emissivity near 1.0. The effective volume of the metabolic chamber was calculated according to Bartholomew et al. (1981) and was 2,660 mL in the absence of a bird. Helox was then passed through the chamber at metered rates, and oxygen consumption ($\dot{V}_{O_2}$) was measured (see below). The metabolic chamber was placed inside an environmental chamber capable of regulating temperature $\pm 0.5°C$. Metabolic chamber temperature was monitored continuously throughout cold-stress tests with an Omega thermocouple thermometer (model Omni IIB, previously calibrated to a thermometer traceable to the U.S. Bureau of Standards) attached to a 30-gauge copper-constantan thermocouple inserted into the inlet port of the metabolic chamber approximately 5 cm above the bird's head. The metabolic chambers was periodically checked for leaks using a soap and water solution. No leaks were detected in the system.

Temperatures for cold stress were 6°, 3°, and 0°C in summer and 0°, −3°, −6°, −9°, and −12°C in winter. The lower temperatures at each season caused a majority of individuals to become hypothermic. Previous studies documenting M_{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, 1993). Individual birds were exposed to a single temperature within the series for 65 min or until they became hypothermic (indicated by a steady decline in $\dot{V}_{O_2}$ over 3 min). For titmice, four individuals were tested at a random second temperature within the series approximately 24 h after their first cold-stress test. This is because they became hypothermic at −12°C within 15 min, which gave no usable data. At the termination of each cold-stress test, birds were quickly removed from the chamber, and body temperature (T_b [$\pm 0.1°C$]) was recorded within 30 s with a 30-gauge copper-constantan thermocouple attached to an Omega model HH25-TC thermometer (previously calibrated to a thermometer traceable to the U.S. Bureau of Standards). If it took longer than 30 s to record body temperature, the data were discarded since small birds can rewarm rapidly. The thermocouple was inserted into the cloaca to a depth where further insertion did not alter temperature reading (approximately 10–12 mm). Birds with a cloacal temperature less than 37°C were considered hypothermic.

Summit Metabolic Rate

Once a bird was in the chamber, I measured $\dot{V}_{O_2}$ during helox cold stress using open-circuit respirometry. Dry, CO_2-free helox from compressed gas cylinders was drawn through the metabolic chamber using a diaphragm pump. Outlet flow rates of 1,096–1,118 mL min^{-1} were maintained by a Matheson precision rotameter (model 604), calibrated with helox to $\pm 1\%$ volumetrically (Brooks vol-u-meter, Brooks Instrument Division, Hatfield, Pa.), located downstream from the metabolic chamber. These flow rates yielded changes in oxygen content between influx and efflux gas of 0.3%–0.7% and maintained oxygen content of efflux gas above 20.2%. In addition, these flow rates allowed the gas mixture within the metabolic chamber to reach 99% equilibrium in $\simeq 11$ min, as calculated using the equation of Lasiewski et al. (1966). Fractional concentration of oxygen in dry, CO_2-free efflux gas was determined from a 100 mL min^{-1} subsample using an Ametek model S-3A oxygen analyzer (Pittsburgh). Measurements of dry, CO_2-free efflux gas were recorded every 10 s on a computer using Datacan 5.0 data collection and analysis software (Sable Systems International, Henderson, Nev.). Oxygen consumption values were calculated according to the method of Bartholomew et al. (1981). I analyzed M_{sum} data according to Dawson and Smith (1986) by averaging $\dot{V}_{O_2}$ over consecutive 10-min intervals (1–10, 2–11, etc.). The highest 10-min mean $\dot{V}_{O_2}$ was considered M_{sum} at the test temperature. The first 15 min of $\dot{V}_{O_2}$ measurements were omitted from calculations in order for efflux oxygen concentration readings to stabilize. Tests were conducted on the day of capture or on the day after capture from 1100 to 1700 hours (MST).

Basal Metabolic Rate Measurements

Procedures used to measure BMR were similar to those for M_{sum} except that air was used rather than helox. For BMR, chamber temperature ranged from 20° to 30°C, which is within the thermal neutral zone for both the mountain chickadee and juniper titmouse (Cooper 1998). BMR was measured from 2200 to 0300 hours in summer and from 2100 to 0400 hours (MST) in the winter. Birds were fasted for at least 4 h before testing to insure postabsorptive conditions. Dry, CO_2-free air was drawn through the metabolic chamber at outlet flow rates of 442–450 mL/min. After a 1-h equilibration period, metabolic rates were determined as the mean $\dot{V}_{O_2}$ over a 60-min period. Oxygen consumption was calculated as steady-state $\dot{V}_{O_2}$ using equation 4a of Withers (1977). All values for $\dot{V}_{O_2}$ were corrected for STP.

Statistics

All means are presented with their corresponding standard deviations. In order to determine M_{sum}, I compared $\dot{V}_{O_2}$ of more

than two groups using one-way ANOVA. Seasonal means of cold endurance, M_{sum}, and BMR were compared using two-tailed Student's t-tests as variances and were not significantly different (F-tests for equality of variances). All data are presented on a whole-organism basis because this may be more instructive when doing seasonal comparisons (Dawson and Smith 1986; Swanson 1991a), and it avoids confounding effects of ratios (Packard and Boardman 1999). The effect of helox T_a on T_b was analyzed by least squares regression. Birds that became hypothermic in less than 25 min had substantially lower M_{sum} than birds that remained normothermic for longer periods and were omitted from calculations of mean M_{sum} (Koteja 1986). Statistical significance was accepted at $P < 0.05$. All statistics were computed with SPSS 6.1 (SPSS, Chicago).

Results

Body Mass and Condition

Mean morning mass at capture for chickadees was significantly lower in winter than summer ($t = 2.66$, $P < 0.01$). Mean morning mass at capture for titmice did not vary seasonally ($t = 0.38$, $P = 0.71$; Table 1).

Visible fat depots in furcular and abdominal regions did not vary seasonally in titmice (furcular: $t = 0.38$, $P = 0.71$; abdominal: $t = -0.41$, $P = 0.68$). Winter chickadees had significantly higher furcular fat scores than in summer ($t = -2.41$, $P < 0.05$) but did not vary seasonally in abdominal fat scores ($t = -1.58$, $P = 0.11$). Fat content did not vary seasonally in chickadees ($t = 0.08$, $P = 0.94$) or titmice ($t = 0.25$, $P = 0.81$; Table 1).

Contour plumage mass in winter was significantly higher in chickadees ($t = -6.65$, $P < 0.001$) and in titmice ($t = -4.06$, $P < 0.001$).

Winter contour plumage mass represents increases of 104% and 46% over summer contour plumage mass in chickadees

and titmice, respectively (Table 1). Pectoralis mass was significantly higher in winter chickadees ($t = -2.60$, $P = 0.02$) and in winter titmice ($t = -2.75$, $P = 0.25$) compared to their summer counterparts (Table 1).

Cold Tolerance and Body Temperature

Both species were tolerant of colder helox temperatures in winter than in summer (Fig. 2). For example, greater than 50% of all summer chickadees and titmice became hypothermic from 0° to 6°C, while in winter it took temperatures from −6° to −12°C to induce hypothermia in greater than 50% of all individuals tested. In winter, titmice were unable to tolerate helox cold stress at −12°C ($n = 4$) for more than 15 min and were omitted from M_{sum} calculations. The average time it took for summer birds to become hypothermic in helox was 38.0 min for chickadees ($n = 19$) and 42.0 min for titmice ($n = 13$). In winter, the average time it took to become hypothermic in helox was 44.8 min for chickadees ($n = 24$) and 37.5 min for titmice ($n = 13$). For chickadees, the increased time to hypothermia in winter relative to summer was not significant ($t = -1.34$, $P = 0.19$).

Mean T_b of normothermic birds after helox cold stress in summer birds was $37.7° \pm 0.6°$C ($n = 7$) for chickadees and $38.3° \pm 1.1°$C ($n = 10$) for titmice. For winter birds, mean T_b of normothermic birds after helox cold stress was $37.9° \pm 1.1°$C ($n = 3$) for chickadees and $37.7° \pm 0.5°$C ($n = 3$) for titmice. For birds remaining normothermic throughout helox cold-stress tests, T_b was independent of T_a in helox (summer: chickadees, $r^2 = 0.003$, $F = 0.02$, $P = 0.91$; titmice, $r^2 = 0.25$, $F = 2.60$, $P = 0.15$; winter: chickadees, $r^2 = 0.21$, $F = 0.27$, $P = 0.70$; titmice, $r^2 = 0.43$, $F = 0.75$, $P = 0.55$).

Cold tolerance may be influenced by seasonal variation in thermal conductance; therefore, thermal conductance was calculated for individual birds using the equation $C =$

Table 1: Seasonal values of morning body mass and composition for mountain chickadees and juniper titmice

Measurement	Summer		Winter	
	Chickadees	Titmice	Chickadees	Titmice
Body mass (g)	$11.2 \pm .68$ (50)	$16.9 \pm .80$ (20)[a]	$10.8 \pm .77$ (46)[b]	$16.8 \pm .97$ (13)[a]
Fat content (g)	$.36 \pm .09$ (8)	$.77 \pm .18$ (4)	$.36 \pm .13$ (7)	$.72 \pm .34$ (4)
Visible fat:				
Furcular	$.06 \pm .24$ (50)	$.19 \pm .54$ (16)	$.29 \pm .58$ (46)[b]	$.11 \pm .33$ (9)
Abdominal	$.22 \pm .42$ (50)	$.06 \pm .25$ (16)	$.39 \pm .61$ (46)	$.11 \pm .33$ (9)
Lean dry mass (g)	$2.84 \pm .23$ (8)	$4.88 \pm .39$ (4)	$2.79 \pm .37$ (7)	$4.41 \pm .40$ (4)
Body water (g)	$8.17 \pm .80$ (8)	$11.23 \pm .84$ (6)	$8.24 \pm .99$ (7)	11.62 ± 1.90 (4)
Contour plumage mass (g)	$.28 \pm .08$ (7)	$.46 \pm .09$ (6)	$.57 \pm .09$ (7)[b]	$.67 \pm .05$ (4)[b]
Pectoralis mass (g)	$.78 \pm .14$ (8)	$.80 \pm .13$ (6)	$1.04 \pm .24$ (7)[b]	$.98 \pm .15$ (4)[b]

Note. Sample size is given in parentheses. All data are reported as means ± SD.

[a] There were three additional titmice tested in both summer and winter for which morning body mass was not recorded.

[b] Indicates significant difference in seasonal intraspecific comparisons ($P < 0.05$).
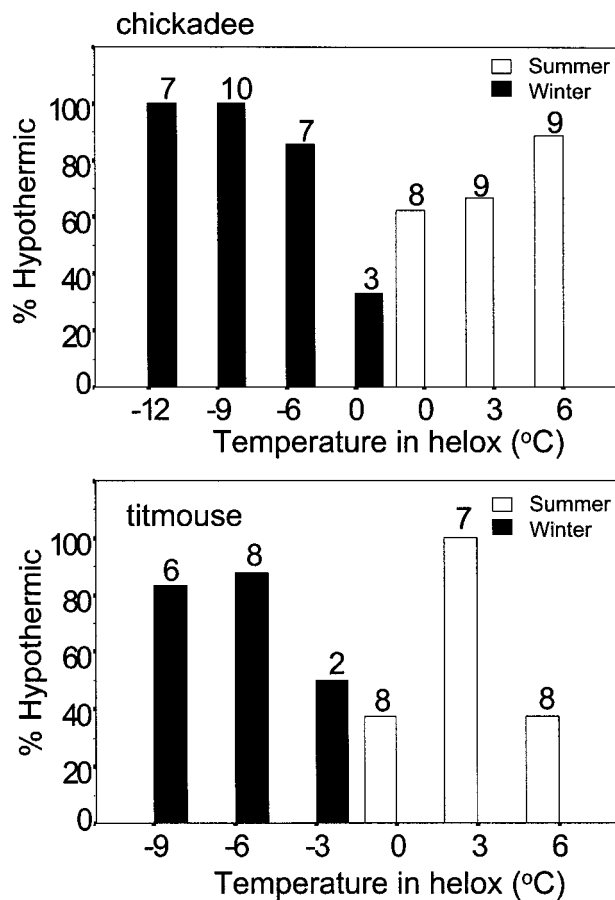
Figure 2. Cold tolerance for seasonally acclimatized mountain chickadees and juniper titmice over the 65-min test period. Bars represent percentage of individuals that became hypothermic. Numbers above bars indicate sample size.

$M_{sum}/(T_b - T_a)$ (Scholander et al. 1950). Thermal conductance was calculated using the M_{sum} and T_b for each individual measured at each test temperature. Thermal conductance for chickadees varied significantly between summer (7.97 ± 1.46 mL O_2 h^{-1} $°C^{-1}$, $n = 25$) and winter (6.61 ± 1.44 mL O_2 h^{-1} $°C^{-1}$, $n = 22$, $t = 3.21$, $P < 0.01$). Conductance for titmice did not vary significantly between summer (8.56 ± 0.92 mL O_2 h^{-1} $°C^{-1}$, $n = 22$) and winter (8.35 ± 1.57 mL O_2 h^{-1} $°C^{-1}$, $n = 15$, $t = 0.53$, $P = 0.60$).

Summit Metabolic Rate

M_{sum} varied seasonally in chickadees and titmice, with maximum values occurring in winter (Table 2). For chickadees, M_{sum} did not vary with helox temperatures during summer, and M_{sum} represents pooled values over the 0°–6°C range tested ($F_{2,23} = 0.09$, $P = 0.92$; Fig. 3). For summer titmice, M_{sum} did vary with helox temperatures ($F_{2,20} = 6.15$, $P < 0.01$). Pairwise

mean comparisons were made using Tukey's test, and birds at 0°C had significantly higher M_{sum} than at 6°C. However, birds at 0°C were not different from those at 3°C, and birds at 3°C were not significantly different from those at 6°C. Therefore, I pooled M_{sum} over the helox temperature range for summer titmice (Fig. 3). In winter titmice, $\dot{V}o_2$ did not vary with helox temperatures, and M_{sum} represents pooled values over the $-3°$ to $-9°C$ temperature range ($F_{2,13} = 1.23$, $P = 0.32$). For winter chickadees, $\dot{V}o_2$ varied significantly with helox temperature ($F_{3,23} = 5.32$, $P < 0.01$). Pairwise mean comparisons using Tukey's test showed that $\dot{V}o_2$ was significantly higher at $-9°C$ compared with other test temperatures, and this rate was used as the M_{sum} (Fig. 3).

Winter chickadees had higher M_{sum} ($t = 2.71$, $P = 0.001$) than summer chickadees. Winter titmice also had higher M_{sum} relative to summer titmice ($t = 3.05$, $P = 0.004$; Table 2).

Basal Metabolic Rate

Both species had significantly greater BMR in winter than in summer. BMR for winter chickadees ($n = 17$) was significantly higher relative to summer chickadees ($n = 14$, $t = 2.21$, $P = 0.035$). The BMR ($t = 3.89$, $P < 0.001$) for winter titmice ($n = 12$) was higher than for summer titmice ($n = 16$; Table 2). Factorial increments in BMR were 1.17 in winter for chickadees and 1.22 for titmice. BMR exceeded allometrically predicted values (Aschoff and Pohl 1970) by 9.6% for summer chickadees and 27.4% for winter chickadees. For summer titmice, BMR was 2.4% lower than allometric predictions and 12.8% lower than BMR in juniper titmice from southeastern Arizona (Weathers and Greene 1998). For winter titmice, BMR was 13.1% higher than allometrically predicted.

Discussion

Body Mass and Composition

Juniper titmice in this study did not show seasonal variation in morning body mass, visible fat, or fat content. The decreased morning body mass of winter-acclimatized mountain chickadees was probably due to increased length of overnight fasting compared to summer. Evening body masses for chickadees during BMR tests were equivalent in summer and winter chickadees (Table 2). Although visible fat in the furcular region was increased in winter compared with summer for chickadees, overall fat content did not vary seasonally. Increased body mass and fat stores are a common pattern of many cold-temperate wintering passerines, enabling these birds to meet thermoregulatory demands and buffer against temporary foraging restriction due to inclement weather (King 1972; Dawson and Marsh 1986; Waite 1992; O'Connor 1995). However, the body mass and fat scores of tree-foraging birds typically change little seasonally compared with ground-foraging birds. This is associated with more predictable food supplies in tree-foraging

Table 2: Body mass and whole-organism metabolic rates for seasonally acclimatized mountain chickadees and juniper titmice from northern Utah

Species	Body Mass (g)	BMR	Body Mass (g)	M_{sum}	M_{sum}/BMR
Chickadee:					
Summer	11.1 ± 1.1 (14)	.69 ± .14	11.4 ± .9 (26)	4.26 ± .77	6.2
Winter	11.1 ± 1.1 (17)	.81 ± .17[a]	11.0 ± .9 (10)	5.37 ± .77[a]	6.6
Titmouse:					
Summer	16.1 ± .8 (16)	.81 ± .09	16.2 ± 1.2 (23)	4.82 ± .51	6.0
Winter	17.2 ± 1.1 (12)[a]	.99 ± .16[a]	17.0 ± 1.1 (16)[a]	5.60 ± 1.00[a]	5.7

Note. All data are reported as means ± SD. Whole-organism metabolic rates are measured in milliliters O_2 per minute. Body masses are means for the treatment group. Parenthetical values following body mass are sample sizes of the treatment groups.

[a] Indicates significant difference in seasonal intraspecific comparisons ($P < 0.05$).
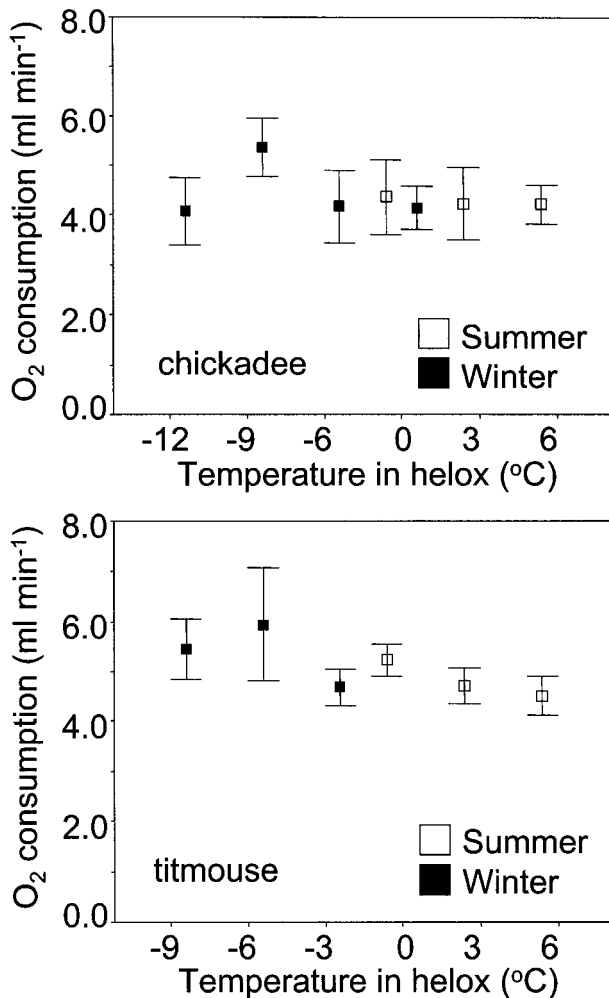

Figure 3. Whole-organism metabolism (mL O_2 min^{-1}) at various helox chamber temperatures for mountain chickadees (*top*) and juniper titmice (*bottom*). Means and 95% confidence intervals are shown at each temperature.

birds compared with ground-foraging birds (Rogers 1987; Rogers and Smith 1993). In addition, chickadees and titmice cache food in the fall for use in the winter (Bent 1946; Haftorn 1974). Therefore, minor seasonal changes in body mass in chickadees and titmice in this study agree with the findings of Rogers (1987).

Chaplin (1974) found winter increases in fat in black-capped chickadees from New York that were trapped in the afternoon. Consequently, seasonal variation in fat content in this study may have been underestimated. However, in several cold-temperate wintering passerines, significant winter increases in fat also occur in morning-captured birds (Dawson and Carey 1976; Swanson 1991*a*; Waite 1992; O'Connor 1995). This suggests that chickadees and titmice do not store fat in winter to the same degree as some other cold-temperate wintering passerines and that seasonal increases in fat stores are not a principal component of winter acclimatization in these birds.

Cold Tolerance and Thermal Conductance

Both species were tolerant of colder test temperatures in winter compared with summer. Thus, cold tolerance of both species appears to improve in winter (Fig. 2). Because test temperatures used in summer and winter were different from one another (except for chickadees at 0°C), care should be used in these comparisons of cold tolerance . However, improved cold tolerance in winter-acclimatized birds is widespread in cold-temperate wintering species and is generally associated with increased thermogenic capacity (Marsh and Dawson 1986; Dawson and Marsh 1989; Swanson 1990; Cooper and Swanson 1994; O'Connor 1995; Liknes and Swanson 1996). Although cold exposure endurance did not increase significantly in these two species, increased cold tolerance is likely attributable to increased shivering endurance, which is closely linked to increased M_{sum} (Marsh and Dawson 1989*b*; Bennett 1991; Swanson 2001). I estimated air temperature equivalents for helox test temperatures by inserting M_{sum} into equations relating $\dot{V}o_2$ to T_a below thermoneutrality (Cooper 1998) and solving

Table 3: Enhancement of thermal conductance in helox compared to air for passerines

Species	C_{helox}/C_{air}	Reference
Common redpoll (*Carduelis flammea*)	2.6	Rosenmann and Morrison 1974
American goldfinch (*Carduelis tristis*)	2.7	Dawson and Smith 1986
House sparrow (*Passer domesticus*)	1.72	Koteja 1986
Dark-eyed junco (*Junco hyemalis*)	3.0	Swanson 1990
Black-capped chickadee (*Poecile atricapillus*)	2.84	Cooper and Swanson 1994
Mountain chickadee (*Poecile gambeli*)	2.50[a]	This study
Juniper titmouse (*Baeolophus griseus*)	2.69[a]	This study

[a] Average of summer and winter C_{helox}/C_{air} values.

for T_a. Estimated air temperatures ranged from $-35.6°$ to $-69.3°C$ for summer birds and from $-63.1°$ to $-92.6°C$ for winter birds. This illustrates that both species are capable of tolerating acute cold exposure well below temperatures experienced under natural conditions.

In winter, thermal conductance in helox was 17% lower in chickadees than in summer. This indicates that winter chickadees are better insulated than their summer counterparts. Thermal conductance did not vary in titmice, indicating seasonally stable insulation. This suggests that chickadees have better insulation in winter, probably as a result of their increased contour plumage mass, but that increased contour plumage mass in titmice does not increase insulation. The increased contour plumage mass in titmice may provide better insulation in their natural environment, which includes forced convection due to wind. Thermal conductance in helox exceeded thermal conductance in air (Cooper 1998) in summer by 2.46 times in chickadees and by 2.90 times in titmice and in winter by 2.66 times in chickadees and by 2.47 times in titmice. These values are similar to factorial increments in minimal thermal conductance induced by helox cold stress in other temperate wintering passerines (Table 3). High factorial increments in minimal thermal conductance by helox cold stress indicate that heat loss in small birds is limited mainly by plumage insulation rather than body tissues such as subcutaneous fat (Dawson and Smith 1986). In addition, these values indicate that the importance of plumage insulation in chickadees and titmice is not markedly increased relative to other temperate wintering birds.

Summit and Basal Metabolic Rates

Both species had significantly elevated BMR and M_{sum} in winter compared with summer. Increased BMR and M_{sum} in winter for both chickadees and titmice demonstrate that metabolic adaptations are important components of winter acclimatization in these species. BMR varies seasonally in some passerines (Pohl and West 1973; Weathers and Caccamise 1978; Swanson 1991a; Cooper and Swanson 1994; Liknes and Swanson 1996) but not in others (Dawson and Carey 1976; Dawson et al. 1985; O'Connor 1995; Sharbaugh 2001).

In this study, pectoralis mass increased significantly in winter compared with summer for both chickadees and titmice. The 33.3% increase in pectoralis mass in chickadees parallels a 26.1% increase in M_{sum} and a 17.4% increase in BMR in chickadees. The 24.1% increase in pectoralis mass parallels a 16.2% increase in M_{sum} and a 22.2% increase in BMR in titmice. These data suggest that the winter increase in BMR for both species is at least partly due to the increased metabolic machinery of the pectoralis mass, which is needed for increased thermogenic capacity (Swanson 1991b). Pectoralis mass has also been found to be strongly correlated with BMR in house sparrows (Chappell et al. 1999). Similar increases in winter pectoralis muscle mass have been found in dark-eyed juncos (Swanson 1991b) and house finches (O'Connor 1995) and appear to be associated with increased M_{sum} in these species. However, in house finches, BMR was seasonally stable in spite of increased pectoralis muscle mass in winter (O'Connor 1995). The possible adaptive significance and mechanistic basis of increased winter BMR in birds is not certain. Increased pectoralis mass in winter may be more important for elevation of M_{sum} than BMR. If mass-specific aerobic capacity remains seasonally static in chickadees and titmice, as reported for some other passerines (Marsh 1981; Yacoe and Dawson 1983), then any winter increase in pectoralis mass represents an increase in overall aerobic capacity. Even in birds that have a significantly higher mass-specific aerobic capacity in winter, the increase is generally low ($\sim$7%). Thus, an increase in pectoralis mass may provide the most significant increase in overall thermogenic capacity in winter birds.

Winter M_{sum} on a whole-organism basis exceeds summer M_{sum} by 26.1% in chickadees and by 16.2% in titmice. These values are within the range of winter increases in M_{sum} in other passerines, which range from 0% to 52% greater than summer values (Marsh and Dawson 1989a; Liknes and Swanson 1996). The winter elevation of M_{sum} for mountain chickadees is similar to the 36% increase in M_{sum} recorded for winter black-capped chickadees (Cooper and Swanson 1994). M_{sum} in summer was 5.0% lower for chickadees and 16.2% lower for titmice than allometrically predicted values. M_{sum} in winter was 19.9% higher for chickadees and 6.7% lower for titmice than predicted using the allometric equation of Dutenhoffer and Swanson (1996),

which was derived using M_{sum} values for spring-, summer-, and winter-acclimatized passerines. These allometric comparisons of M_{sum} demonstrate that winter chickadees are capable of markedly increased M_{sum} compared with other passerines, but winter titmice are below predicted values from other temperate wintering passerines.

The increase in M_{sum} in winter birds contrasts to data on house finches tested in Colorado at an elevation of 1,671 m. Colorado house finches have seasonally static M_{sum}. O'Connor (1996) states that the lack of seasonal variation in M_{sum} in Colorado house finches may reflect direct physiological adjustments to altitude or indirect effects of high climatic variability associated with altitude. In either case, chickadees and titmice in this study that were captured and tested at high altitudes have seasonal variation in M_{sum} that is similar to other species tested from lower altitudes.

Metabolic expansibilities (M_{sum}/BMR; Dawson and Carey 1976) for chickadees and titmice (Table 2) are similar to those recorded for black-capped chickadees in summer (6.7 times) and winter (7.9 times) and are among the highest recorded for birds, which range from 3.3 to 8.4 times (Marsh and Dawson 1986; Saarela et al. 1989; Lopez-Calleja and Bozinovic 1995; Dutenhoffer and Swanson 1996; Liknes and Swanson 1996).

These metabolic expansibilities demonstrate that mountain chickadees and juniper titmice are capable of elevating metabolism to a substantial degree to compensate for high rates of heat loss at cold winter temperatures. In addition, these metabolic expansibilities demonstrate that chickadees and titmice are able to elevate metabolism under cold stress in spite of behavioral adaptations such as food caching and using regulated nocturnal hypothermia (Bent 1946; Cooper 1998).

Acknowledgments

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