

SEASONAL ENERGETICS OF MOUNTAIN CHICKADEES AND JUNIPER TITMICE¹

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Abstract. I used behavioral, meteorological, and laboratory metabolism data to calculate daily energy expenditure (DEE) in seasonally acclimatized Mountain Chickadees (*Poecile gambeli*) and Juniper Titmice (*Baeolophus griseus*). Analyses of laboratory metabolic data revealed that foraging energy requirements were not significantly higher than alert perching energy requirements. Respective DEE of chickadees and titmice were 48.8 kJ day⁻¹ and 48.3 kJ day⁻¹ in summer and 66.3 kJ day⁻¹ and 98.7 kJ day⁻¹ in winter. DEE as a multiple of basal metabolic rate (BMR) was 2.31 in summer chickadees and 1.91 in summer titmice. DEE was 2.70 times BMR in winter chickadees and 3.43 times BMR in winter titmice. The marked increase in calculated DEE in winter birds compared to summer is in contrast to a pattern of increased DEE in the breeding season for several avian species. These data suggest that winter may be a period of even greater stringency for small birds than previously believed.

Key words: *Baeolophus griseus*, daily energy expenditure, energy metabolism, Juniper Titmouse, Mountain Chickadee, *Poecile gambeli*.

INTRODUCTION

Small passerine birds that overwinter in cold temperate regions require prolonged energy expenditure for regulatory thermogenesis. In addition, the onset of winter decreases foraging time due to shorter days and may reduce the availability of foraging substrates due to heavy snow or ice cover. Concurrently with these seasonal changes in photoperiod and climate, cold temperate-wintering passerines undergo seasonal acclimatization that facilitates thermoregulatory homeostasis. Previous studies of seasonal acclimatization in passerine birds have focused primarily on seasonal variation in basal metabolism, cold tolerance, maximal thermogenic capacity, and substrate metabolism (Dawson and Marsh 1989, Marsh and Dawson 1989a, 1989b). These studies have generally collected metabolic data for individuals over a very short time period (up to a few hours).

Seasonal patterns observed thus far in avian DEE support two alternative hypotheses (Masman et al. 1986, Weathers and Sullivan 1993). The "reallocation hypothesis" predicts little seasonal variation in DEE. The "increased demand hypothesis" holds that breeding results in a sub-

stantial increase in adult energy demand and subsequently, DEE is highest during breeding. DEE during the breeding season typically equals or exceeds that during winter in birds that have been studied. Although energetic demands may not be higher in winter than during other periods of the year, the conditions in which they must be met are much harsher.

Root (1988b) calculated the resting metabolic rate of 14 species whose metabolism as a function of ambient temperature was available from the literature at the minimum January temperature at each species' northern range boundary. That northern boundary metabolic rate (NBMR), which includes basal metabolism (BMR) and thermoregulatory metabolism, is equal to 2.45 times the BMR for each of the 14 species. The total DEE of those birds must be somewhat greater than 2.45 times basal, because the birds must also expend energy for foraging, digestion, and other activities. Thus, birds may be limited to overwintering in regions where they do not have to raise their DEE beyond slightly greater than 2.45 times basal levels. However, this proposed limit of 2.45 has been criticized by Castro (1989) and Repasky (1991). In order to determine the role of DEE on biogeographic patterns in birds, closely related species with different northern range distributions need to be examined.

The Mountain Chickadee (*Poecile gambeli*) and the Juniper Titmouse (*Baeolophus griseus*)

¹ Received 8 September 1999. Accepted 7 April 2000.

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are small, largely nonmigratory passerine birds that occupy regions of western North America. The northern limits of the distributions of Mountain Chickadees and Juniper Titmice lie in northern British Columbia (60°N latitude) and southern Idaho (44°N latitude), respectively (Godfrey 1986, Cicero 1996). These limits coincide with -23°C and -12°C January average minimum isotherms, respectively (Root 1988a). Thus, the DEE of these two species may be important in determining their northern range distribution. In this study I compare the DEE of seasonally acclimatized Mountain Chickadees and Juniper Titmice. I postulated that DEE in seasonally acclimatized birds would not be stable due to increased thermostatic costs in winter and that DEE for titmice would be near or below $2.45 \times \text{BMR}$.

METHODS

STUDY SITE AND SPECIES

The field portions of this study took place between 5–8 February, 1996 for winter measurements, and between 31 July and 3 August, 1996 for summer measurements. Field data for Mountain Chickadees were recorded in the Bear River Mountains, Cache County, Utah (41°52'N, 111°34'W) at an elevation of 2,200 m. The study site consisted of mixed conifers and quaking aspen (*Populus tremuloides*). Field data for Juniper Titmice were recorded in the Raft River Mountains, Box Elder County, Utah (41°50'N, 113°25'W) near Rosette, Utah at an elevation of 1,850 m. The study site primarily consisted of Utah juniper (*Juniperus osteosperma*) with sparsely scattered singleleaf pinyon pine (*Pinus monophylla*). The titmouse study site is at the northern edge of their range (Cicero 1996).

TIME-ACTIVITY BUDGETS

I collected 16 time-budget samples totaling 67 min of observation for summer chickadees and 16 time-budget samples totaling 87 min of observation for winter chickadees. I collected nine time-budget samples totaling 60 min of observation for summer titmice and eight time-budget samples totaling 80 min of observation for winter titmice. Samples were distributed throughout the day in order to achieve uniform coverage of the birds' active day. I observed focal individuals for 2–30 min (mean \pm SE = 5.3 ± 0.4) and recorded the time spent in three activities (perching, foraging, or flying). Perching includ-

ed singing and grooming. I cannot be certain that each of my time-budget samples for Mountain Chickadees within one season was of a different individual because not all birds observed were banded. However, I made a conscious effort to avoid sampling the same individual twice within a season and to sample as many individuals within a 3.2 km² area per study site. In addition, Juniper Titmice adults remain in pairs year-round and also maintain year-round territories (Dixon 1949). Thus, I was able to observe both banded and unbanded pairs within their own territories for relatively long periods of time.

METEOROLOGY

Concurrent with my time-budget measurements, I monitored the birds' diurnal thermal environment with a meteorological station. Microclimate sensors were mounted on metal poles and were placed 2 m above ground level (snow level in winter) within 25 cm of a tree trunk. The 2-m height was chosen as typical foraging/perching sites from field observations in 1993 to 1996. This is especially important for wind speed measurement because wind profiles vary with height measured from the ground (Campbell and Norman 1998). For Mountain Chickadees, I placed the meteorological station near subalpine fir (*Abies lasiocarpa*), and for Juniper Titmice, I placed the meteorological station near Utah juniper. These trees were the most frequently used for foraging by the respective bird species (pers. observ.). Meteorological variables measured were: (1) air temperature (T_a) (with a shaded 36-gauge copper-constantan thermocouple), (2) operative temperature (T_o) (with a 3.5-cm diameter copper sphere thermometer painted flat gray; Bakken et al. 1985, Walsberg and Weathers 1986), and (3) wind speed (u) (with a Thornwaite model 901 cup anemometer). Sensor outputs were monitored at 60-sec intervals, averaged every 60 min, and recorded with a Campbell Scientific CR10 electronic datalogger. Thermocouples were calibrated with a thermometer traceable to the U.S. Bureau of Standards. The cup anemometer was factory calibrated.

Details of nocturnal microclimate measurement can be found in Cooper (1999). In brief, for nocturnal microclimate measurement, I used T_{es} measured inside nest boxes occupied by a single bird for both chickadees and titmice. Wind speed was measured on different nest box-

es which did not contain a bird and was always zero.

LABORATORY METABOLISM MEASUREMENTS

I measured the metabolic heat production of chickadees and titmice by measuring their oxygen consumption ($\dot{V}O_2$) at stable air temperatures between -10° and 30°C . The birds used in these measurements were captured during summer and winter of 1995 and 1996. Birds were transported from the field to Logan, Utah, where they were housed in individual cages ($0.3 \times 0.3 \times 0.3$ m) and held in a temperature-controlled environmental chamber ($3 \times 3 \times 2.5$ m) for a maximum of one week. The chamber temperature and photoperiod were programmed to follow a cycle that approximated the season and study site to which the birds had been accustomed. While in captivity, birds were provided with food (*Tenebrio* larvae and wild bird seed) and water as needed. Birds tested from 1 June to 25 August were designated "summer birds," and those tested from 20 November to 10 February were designated "winter birds." Oxygen consumption was not measured for any summer birds that were noticeably molting.

I measured $\dot{V}O_2$ during the active phase of the daily cycle on fed birds at rest in darkened metabolism chambers to estimate energetic costs of daytime maintenance plus the cost of alert perching, and on fed birds in metabolism chambers (equipped with a dish of wild bird seed) exposed to normal fluorescent room lighting to estimate energetic costs of daytime maintenance plus the cost of foraging. Nighttime maintenance-energy requirements were estimated from previous $\dot{V}O_2$ measurements during the rest phase on fasted birds resting in the dark (minimum of 4 hr since last meal) (Cooper 1998).

Measurements were made on individual birds using a 3.8 L metabolic chamber fashioned from a paint can. The inside of the metabolic chamber was painted flat black to provide an emissivity near 1.0. Metabolic chamber temperature was regulated within $\pm 0.5^\circ\text{C}$ by placing it in a temperature-controlled environmental chamber. Metabolic chamber temperature was monitored continuously throughout each test 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 in-

serted into the inlet port of the metabolic chamber. Individuals were weighed and then placed inside the metabolic chamber where they perched on 1-cm wire mesh placed 3 cm above a 1-cm layer of paraffin oil used for the collection of fecal material. Oxygen consumption ($\dot{V}O_2$) was then measured using open-circuit respirometry with an Ametek Model S-3A oxygen analyzer (AEI Technologies, Pittsburgh, Pennsylvania). Air was drawn through the metabolic chamber with a diaphragm pump and was dried with indicating Drierite (anhydrous CaSO_4) and scrubbed of CO_2 with Ascarite. Outlet flow rates of dry, CO_2 -free air were maintained at 442–450 mL min^{-1} by a Matheson precision rotameter (Model 604), which was calibrated to $\pm 1.0\%$ (Brooks vol-u-meter), and located downstream from the metabolic chamber. These flow rates yielded changes in oxygen content between influx and efflux gas of 0.3 and 0.7%, and maintained oxygen content of efflux gas above 20.2%. Fractional concentration of oxygen in efflux gas was determined from a 100 mL min^{-1} subsample passed through the oxygen analyzer. Measurements of the efflux gas were recorded every 15 sec on a computer using Datacan 5.0 data collection and analysis software (Sable Systems International, Henderson, Nevada). Evaporative water loss (EWL) was determined over a 60-min timed interval by measuring the increase in mass of a downstream absorbent train containing Drierite. Low permeability Bev-a-Line tubing was used to connect the metabolism chamber to the downstream absorbent train. All weighings were made on an analytical balance (Mettler H51AR). At the end of each metabolism trial, birds were removed from the chamber and body temperature (T_b) ($\pm 0.1^\circ\text{C}$) was recorded by inserting a 30-gauge copper-constantan thermocouple into the cloaca to a depth (approximately 10–12 mm) where further insertion did not alter temperature reading.

$\dot{V}O_2$ and EWL were measured on individual birds exposed to a single randomized temperature in the dark and also in normal room lighting. Individuals were given 24-hr rest in between $\dot{V}O_2$ measurements. All individuals were tested within one week of capture. Individual birds were placed in the metabolic chamber for a total of 2 hr. The first hour was an equilibration time and $\dot{V}O_2$ was measured over the last 60-min of the trial. Oxygen consumption was calculated as steady state $\dot{V}O_2$ using Eq. 4a of

Withers (1977). All values were adjusted to STP. Rates of metabolic heat production were calculated assuming that 20.1 kJ of heat were produced per liter of oxygen consumed for both fed and fasted birds (Gessaman and Nagy 1988).

TIME-ACTIVITY LABORATORY ESTIMATE OF DEE

I calculated the DEE of seasonally-acclimatized chickadees and titmice using time-budget, meteorological, and laboratory metabolism data from the following equation:

$$DEE = (t_{\rho} \dot{H}_m) + (t_{ap} \dot{H}_{ap}) + (t_{fo} \dot{H}_{fo}) + (t_{fl} \dot{H}_{fl}) \quad (1)$$

where t represents duration (in hours) of the activity phases and of the type of activity, and \dot{H} is the energy requirements for a given activity (in kJ hr⁻¹). The subscripts represent the time of day (ρ = nighttime) or the type of activity (m = maintenance metabolism, ap = active perch, fo = foraging, and fl = flight). In equation (1), the first bracketed term, nocturnal energy expenditure, consists of basal and thermoregulatory energy requirements of a sleeping bird. The second bracketed term represents maintenance-energy requirements plus active perching-energy requirements of a daytime bird. The third bracketed term represents maintenance-energy requirements plus foraging-energy requirements of a daytime bird. The second and third bracketed terms subsume thermoneutral and thermoregulatory energy requirements during the bird's active phase and includes the heat increment of feeding (HI). The fourth bracketed term represents flight-energy requirements of a daytime bird. I used Carlson and Moreno's (1992) doubly labeled water estimate of short flight costs in Willow Tits (*Poecile montanus*) to determine the energy cost of flight (\dot{H}_{fl}) in eq. (1). Thus, flight costs were calculated as 11.7 times nighttime basal metabolic rate (BMR). BMR data were taken from Cooper (1998). I related laboratory measurements of \dot{H}_m , \dot{H}_{ap} , and \dot{H}_{fo} directly to the 60-min recordings of microclimate measurements associated with each bird's diurnal and nocturnal phases, respectively. In order to determine total daily energy costs of each activity (perching, flight, foraging, nocturnal maintenance) for chickadees and titmice, I subtracted basal metabolism from each activity. Because basal metabolic rate averages 20–25% higher during the active phase of the daily cycle than during the rest phase (Aschoff and Pohl 1970),

I assumed that active phase basal metabolism was 1.2 times BMR for chickadees and titmice in order to correct each activity for the daily cycle.

ESTIMATING ENERGY COSTS UNDER FIELD CONDITIONS

Equation (1) usually provides mean DEE values within 5% of the mean DEE determined by doubly labeled water (DLW) of free-ranging birds, provided certain criteria are met. First, maintenance and activity costs must be determined for the study population(s) at the same season as time budgets are recorded (Weathers and Sullivan 1993). Secondly, maintenance and activity costs must be evaluated under field conditions using heat transfer theory that uses standard operative temperature to calculate thermoregulatory costs (Buttemer et al. 1986, Weathers and Sullivan 1993). I calculated the complex thermal environment encountered by birds in this study by calculating standard operative temperature (T_{es}) on the basis of the measured field T_e and wind speed (u) using Bakken's (1990) generalized passerine T_{es} scale:

$$T_{es} = T_b - (1 + 0.26u^{0.5})(T_b - T_e) \quad (2)$$

I did not use DLW to determine DEE in chickadees and titmice due to the difficulty in recapturing marked individuals within 24 to 48 hr.

STATISTICAL ANALYSES

Time-activity budgets and time-activity laboratory estimates of DEE were compared using Student t -tests because variances were equal (F -tests for equality of variance). Regression lines were fit by the method of least squares. Slopes and intercepts of regression lines were compared by ANCOVA. Significance was determined at the $P < 0.05$ level for all analyses. All analyses were performed with SPSS 6.1 (Norusis 1989). All data are presented as mean \pm SE.

RESULTS

WEATHER

During the summer and winter study period, no precipitation fell. In summer, mean T_e was $15.1 \pm 1.0^\circ\text{C}$ for chickadees and $19.5 \pm 0.9^\circ\text{C}$ for titmice. In winter, mean T_e was $-3.6 \pm 0.5^\circ\text{C}$ for chickadees and $-5.7 \pm 1.2^\circ\text{C}$ for titmice (Fig. 1). These temperatures are within normal T_a ranges for each study site (Utah State Climate Center, Logan, Utah). In summer, mean wind

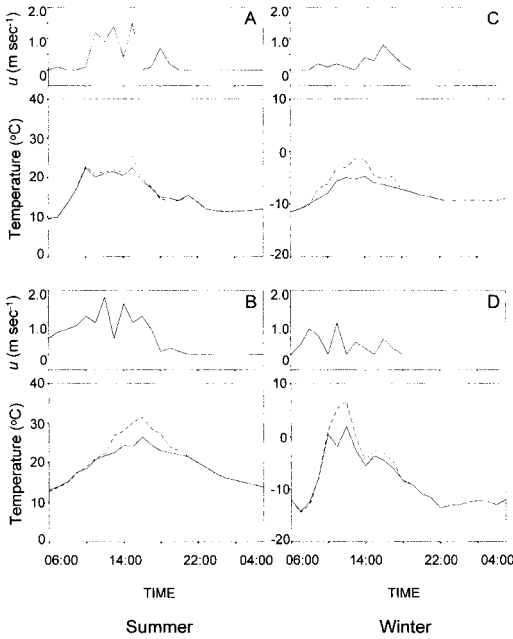


FIGURE 1. Temperature and wind speed (u) for summer Mountain Chickadees (A), summer Juniper Titmice (B), winter Mountain chickadees (C), and winter Juniper Titmice (D). Air temperature (T_a) is represented by solid lines and operative temperature (T_e) is represented by dashed lines.

speed was $0.6 \pm 0.2 \text{ m sec}^{-1}$ for chickadees and $0.9 \pm 0.1 \text{ m sec}^{-1}$ for titmice. In winter, mean wind speed was $0.2 \pm 0.1 \text{ m sec}^{-1}$ for chickadees and $0.3 \pm 0.1 \text{ m sec}^{-1}$ for titmice (Fig. 1).

TIME-ACTIVITY BUDGETS

In summer, chickadees and titmice began foraging around 05:00 and went to roost around 19:00, making their active day about 14 hr long. In winter, chickadees and titmice began foraging around 07:30 and went to roost around 16:30, making their active day about 9 hr long. These

time intervals were used to calculate laboratory estimates of DEE. Chickadees and titmice spend over 50% of their active day foraging in both summer and winter (Table 1). The time budgets of the two species were similar. There were no significant differences either between species or seasonally (Table 1).

LABORATORY METABOLIC RATES

Under the conditions of my laboratory metabolism measurements (isothermal metabolism chamber with no significant shortwave radiation or forced convection), T_a is the same as standard operative temperature (T_{es}). Although normal fluorescent room lighting illuminated the metabolic chamber used to determine foraging costs, this would amount to a negligible amount of irradiance received by the bird due to construction of the chamber. For example, Verdins (*Auriparus flaviceps*) exposed to normal fluorescent room lighting in glass metabolic chambers were subject to an irradiance of $< 3 \text{ W m}^{-2}$ (Wolf and Walsberg 1996). The relationship between oxygen consumption ($\dot{V}O_2$) and standard operative temperature are described for fed summer birds (Fig. 2) and winter birds (Fig. 3).

The comparison of slopes and intercepts by analysis of covariance (ANCOVA) of these regression equations allow comparison of perching and foraging energy costs. For summer chickadees, neither slopes ($F_{1,28} = 1.6, P > 0.2$) nor intercepts ($F_{1,28} = 1.7, P > 0.2$) were significantly different between perching and foraging-energy requirements. For summer titmice, neither slopes ($F_{1,23} = 0.0, P > 0.9$) nor intercepts ($F_{1,23} = 0.0, P > 0.9$) differed between perching and foraging-energy requirements. For winter chickadees, both slopes ($F_{1,24} = 23.2, P < 0.01$) and intercepts were significantly different between perching and foraging costs ($F_{1,24} =$

TABLE 1. Percentage of the active day that seasonally acclimatized Mountain Chickadees and Juniper Titmice spent in various activities. Sample sizes are the number of 2–30 min observations for the indicated focal individuals. t -tests were performed on arcsine transformed percentages.

Percentage of active day spent	Summer		Winter	
	Mountain Chickadees (n = 16)	Juniper Titmice (n = 9)	Mountain Chickadees (n = 16)	Juniper Titmice (n = 8)
Perching	27.5 ± 5.2	34.5 ± 7.3	39.4 ± 6.7	40.5 ± 4.1
Foraging	68.7 ± 4.7	61.5 ± 6.8	53.0 ± 5.4	54.9 ± 5.2
Flying	3.8 ± 0.4	4.0 ± 0.3	7.6 ± 1.2	4.6 ± 0.2

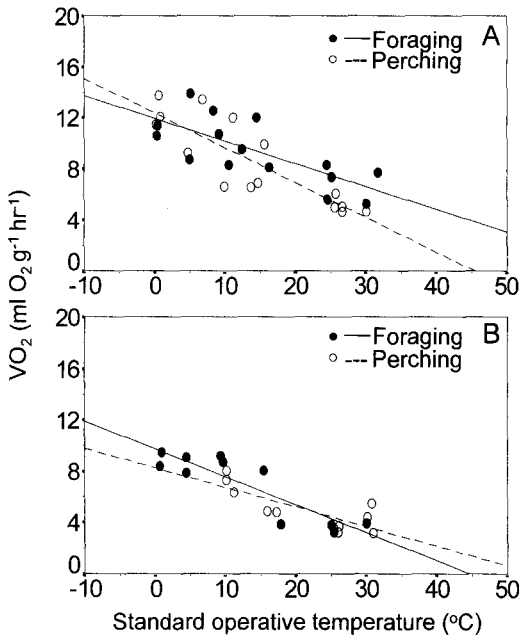


FIGURE 2. Relationship between oxygen consumption and standard operative temperature for summer-acclimatized Mountain Chickadees (A) and Juniper Titmice (B) during the active phase of their daily cycle. Dots represent active birds under lit conditions (foraging) and open circles represent birds under dark conditions (perching). Linear regression equations were, foraging chickadees: $\dot{V}O_2 = 11.97 - 0.18T_{es}$ ($n = 15$, $r^2 = 0.55$, $P < 0.001$), perching chickadees: $\dot{V}O_2 = 12.27 - 0.26T_{es}$ ($n = 16$, $r^2 = 0.72$, $P < 0.001$), foraging titmice: $\dot{V}O_2 = 9.73 - 0.22T_{es}$ ($n = 11$, $r^2 = 0.79$, $P < 0.001$), and perching titmice: $\dot{V}O_2 = 9.63 - 0.21T_{es}$ ($n = 15$, $r^2 = 0.83$, $P < 0.001$).

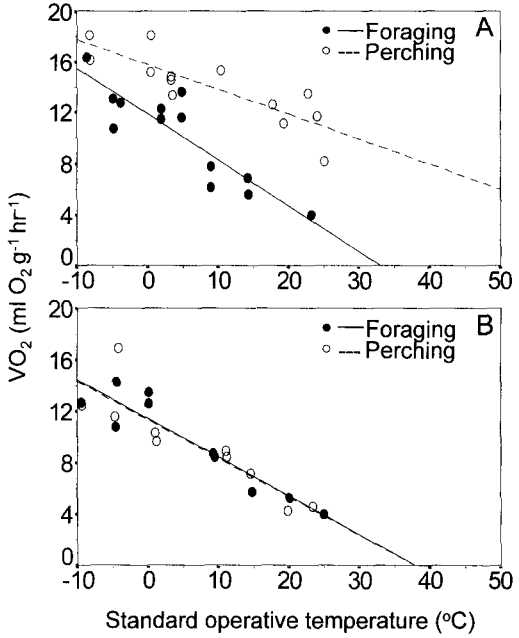


FIGURE 3. Relationship between oxygen consumption and standard operative temperature for winter-acclimatized Mountain Chickadees (A) and Juniper Titmice (B) during the active phase of their daily cycle. Dots represent active birds under lit conditions (foraging) and open circles represent birds under dark conditions (perching). Linear regression equations were, foraging chickadee: $\dot{V}O_2 = 11.91 - 0.36T_{es}$ ($n = 13$, $r^2 = 0.79$, $P < 0.001$), perching chickadees: $\dot{V}O_2 = 15.46 - 0.17T_{es}$ ($n = 14$, $r^2 = 0.64$, $P < 0.001$), foraging titmice: $\dot{V}O_2 = 11.46 - 0.30T_{es}$ ($n = 10$, $r^2 = 0.87$, $P < 0.001$), and perching titmice: $\dot{V}O_2 = 11.39 - 0.30T_{es}$ ($n = 10$, $r^2 = 0.78$, $P < 0.001$).

36.9, $P < 0.001$). For winter titmice, neither slopes ($F_{1,17} = 0.0$, $P > 0.9$) nor intercepts ($F_{1,17} = 0.0$, $P > 0.9$) differed between perching and foraging-energy requirements.

In order to determine the effect of activity on plumage disruption, I calculated overall thermal conductance (K_{cs}) for individuals using the equation of Bakken (1976):

$$K_{cs} = (M - E)/(T_b - T_{cs})$$

where M is metabolic rate and E is evaporative heat loss (assuming 2.429 J of heat for each mg of water evaporated). Thermal conductance values (Table 2) were compared using ANOVA ($F_{7,90} = 7.6$, $P < 0.001$). Pairwise mean comparisons were made using Fisher's LSD; winter

TABLE 2. Thermal conductance ($mW\ g^{-1}\ ^\circ C^{-1}$) for fed birds in lighted conditions (foraging) and for fed birds in dark conditions (perching). Sample sizes are in parentheses.

Condition	Summer		Winter	
	Mountain Chickadees	Juniper Titmice	Mountain Chickadees	Juniper Titmice
Perching	1.44 ± 0.11 (15)	1.04 ± 0.12 (11)	2.20 ± 0.15 (12)	1.52 ± 0.12 (9)
Foraging	1.56 ± 0.11 (14)	1.17 ± 0.12 (9)	1.65 ± 0.13 (13)	1.49 ± 0.15 (8)

TABLE 3. Daily energy budget of seasonally acclimatized Mountain Chickadees and Juniper Titmice as calculated by the TAL method.

Variable (kJ day ⁻¹)	Summer		Winter	
	Mountain Chickadees	Juniper Titmice	Mountain Chickadees	Juniper Titmice
DEE	48.8 ± 0.6	48.3 ± 1.0	66.3 ± 1.5	98.7 ± 0.1
Basal metabolism ^a	23.3 ± 1.0	27.9 ± 1.5	25.4 ± 0.9	27.8 ± 0.4
Nocturnal thermoregulation	6.5 ± 0.1	4.5 ± 0.1	14.5 ± 0.0	32.9 ± 0.0
Alert perching ^b	4.2 ± 1.1	3.8 ± 1.3	10.3 ± 1.0	15.6 ± 0.7
Foraging ^b	9.2 ± 1.0	6.4 ± 0.9	11.3 ± 1.1	17.1 ± 0.6
Flying	5.6 ± 0.7	5.7 ± 1.2	4.8 ± 0.5	5.3 ± 0.1

^a Data are calculated for field conditions incorporating the circadian rhythm in basal metabolism.

^b Data include thermoregulation and heat increment of feeding.

chickadees that were perching had significantly higher thermal conductance than all other birds.

TIME-ACTIVITY LABORATORY (TAL) ESTIMATE OF DEE

Daily energy expenditure estimated by the TAL method averaged 48.8 and 48.3 kJ day⁻¹ for summer Mountain Chickadees and Juniper Titmice, respectively (Table 3). Daily energy expenditure averaged 66.3 and 98.7 kJ day⁻¹ for winter chickadees and titmice, respectively (Table 3). For both chickadees and titmice, DEE was significantly higher in winter compared to summer (chickadees, $t_{30} = 11.0$, titmice, $t_{15} = 34.5$; both $P < 0.001$). Juniper Titmice weighed significantly more than Mountain Chickadees in both summer and winter (Cooper 1998), and the mass difference confounds direct comparison of DEE. However, the difference in body mass can be removed by converting DEE to units of kJ g^{-0.63} day⁻¹, where M^{-0.63} is the interspecific scaling of DEE (Weathers and Sullivan 1989). Using 11.7 g as the mean daily mass of chickadees and 17.4 g for titmice (unpubl. data), I computed the mass-adjusted DEE for summer and winter-acclimatized individuals. Summer chickadees mass-adjusted DEE (10.4 ± 0.13 kJ g^{-0.63} day⁻¹, $n = 16$) was significantly higher than mass-adjusted DEE of summer titmice (8.0 ± 0.16 kJ g^{-0.63} day⁻¹, $n = 9$; $t_{23} = 11.1$, $P < 0.001$). In winter, mass-adjusted DEE was significantly lower for chickadees (14.1 ± 0.3 , kJ g^{-0.63} day⁻¹, $n = 16$) than titmice (16.3 ± 0.1 kJ g^{-0.63} day⁻¹, $n = 8$; $t_{22} = -3.5$, $P < 0.01$).

DISCUSSION

TIME-ACTIVITY BUDGETS

Mountain Chickadees and Juniper Titmice did not increase the percentage of the active day

spent foraging in winter. This is in spite of a 36% and 204% increase in DEE in chickadees and titmice, respectively. This lack of seasonal variation in foraging time suggests that foraging efficiency increases in winter in these species. This is probably due to the availability of food caches stored during the fall by these species (Sherry 1989). However, this lack of seasonal variation in foraging time may also be due to the high amount of time spent caching food in summer birds in this study. For example, predicted foraging time based on Bryant and Westterp (1980) would be 32% and 24% of the active day in summer chickadees and titmice, respectively. Actual time spent foraging in summer birds was 37% higher than predicted for both chickadees and titmice.

ACTIVITY HEAT AND THERMOREGULATION

By comparing the regression equations relating metabolism to T_{es} for fed, daytime birds resting in the dark with those for fed, daytime birds exposed to light, the energetic cost of physical activity can be calculated. In summer chickadees, and both summer and winter titmice, regression equations did not differ significantly. For winter chickadees, the slopes and intercepts were significantly different. Winter chickadees in illuminated chambers had lower metabolism than those resting in the dark. How actively-foraging birds can possibly have lower metabolism than inactive perching birds is unclear. One possible explanation is that perching chickadees became stressed when they were deprived of food during their normal period of foraging activity. These data indicate that heat produced as a by-product of activity substitutes for thermoregulatory requirements and indicates that chickadee and titmouse behavior has no net energy cost at cold

temperatures. A similar circumstance applies to Yellow-eyed Juncos (*Junco phaeonotus*) (Weathers and Sullivan 1993), to the foraging behavior of winter Verdins (Webster and Weathers 1990), and terrestrial locomotion in cold-exposed White-crowned Sparrows (*Zonotrichia leucophrys*) (Paladino and King 1984).

Complete substitution of thermoregulatory demands due to exercise heat in birds may not occur in some birds due to plumage disruption that causes increased thermal conductance (Nomoto et al. 1983). For chickadees and titmice, thermal conductance does not vary between perching and foraging birds (except increased conductance in perching winter chickadees). This demonstrates that very little plumage disruption occurs while foraging in these birds. Lack of plumage-layer disruption has recently been demonstrated in eastern House Finches (*Carpodacus mexicanus*) hopping on a treadmill at 0.5 m sec^{-1} (Zerba et al. 1999). Heat produced as a by-product of activity may substitute for thermoregulatory requirements in birds more regularly than previously believed.

SEASONAL VARIATION IN DEE

Summer DEE values for chickadees and titmice are 86.8% and 63.8%, respectively of predicted DEE based on body mass (Nagy 1987). Winter DEE values for chickadees and titmice are 118.0% and 130.4%, respectively of allometrically predicted DEE (Nagy 1987). Although these winter values exceed allometric predictions, they are within 1% of mass-specific values of DEE for winter-acclimatized Black-capped Chickadees determined using doubly labeled water (Karasov et al. 1992). DEE values from this study are within 8% to 15% of 24-hr metabolism measurements using total collection feeding trials of Mountain Chickadees and Juniper Titmice (unpubl. data). In addition, because heat produced as a by-product of activity substitutes for thermoregulatory requirements in these species, DEE values should not be significantly affected by the relatively small sampling time of perching or foraging activity.

The "increased demand hypothesis" holds that breeding results in a substantial increase in adult energy demand and consequently, DEE is highest during breeding. Data from the present study indicate that winter, due to its increased thermoregulatory costs, represents a substantial energy increase compared to summer. One pos-

sible confounding variable with my study is that I did not collect time-budgets during the peak of the breeding season and therefore do not know whether my TAL DEE calculations would change. However, during the summer period when I collected time budgets, individuals were storing food items, resulting in increased foraging times relative to predicted times and probably resembling foraging times of adults feeding nestlings. For example, the amount of time spent foraging by summer birds in this study is very close to that recorded for Yellow-eyed Juncos feeding nestlings and fledglings (Weathers and Sullivan 1989). In order to estimate whether my DEE calculations would change during the breeding season, I related the equations relating $\dot{V}O_2$ to T_{es} using wind speed from this study (Fig. 1) and mean air temperatures (T_a) from the study sites during May (Utah State Climate Center) to calculate T_{es} . May is when breeding begins in these species (pers. observ.). For activity periods, I used mean maximum T_a , and for resting periods I used mean minimum T_a at the respective study sites. DEE calculated with May climate data is 57.3 kJ day^{-1} in Mountain Chickadees and 53.2 kJ day^{-1} in Juniper Titmice. Thus, DEE may be 10–17% higher in breeding birds. However, these values are still markedly lower than winter values.

The markedly increased DEE in winter relative to summer contrasts with data from most passerines tested to date. For birds where DEE was measured with DLW, only male dippers (*Cinclus cinclus*) and White-crowned Sparrows have increased DEE in winter compared to breeding (Bryant and Tattner 1988, Weathers et al. 1999). All other passerines in which DEE has been measured seasonally have relatively stable DEE or markedly increased DEE during the breeding season (Weathers and Sullivan 1993). Two possible factors may explain the seasonal changes in DEE found in chickadees and titmice in this study. First, the birds in this study were exposed to much colder environmental temperatures, and therefore increasing thermoregulatory costs compared to other birds so far tested (with the exception of dippers) (Bryant and Tattner 1988). Secondly, winter-acclimatized Mountain Chickadees have 13% higher thermal conductance (nighttime values) and winter-acclimatized Juniper Titmice have 26% higher thermal conductance than allometrically predicted (Cooper 1998). Thus, the relatively poor insu-

lation of these birds, especially of titmice, increases their thermoregulatory costs.

ROLE OF DEE ON NORTHERN RANGE LIMITS

DEE as a multiple of basal metabolic rate (BMR) was 2.31 in summer chickadees and 1.91 in summer titmice. DEE was 2.70 times BMR in winter chickadees and 3.43 times BMR in winter titmice. The winter values exceed the suggested northern boundary metabolic rate (NBMR) of 2.45 times BMR. The total DEE of these birds would be expected to be somewhat greater than 2.45 times basal, because the birds must also expend energy for digestion and flight. For winter-acclimatized Siberian Tits (*Poecile cinctus*) and Willow Tits (*Poecile montanus*) tested from their northern January isotherm, DEE was 2.55 and 2.50 times BMR, respectively (Carlson et al. 1993). Thus, data for chickadees and tits appear to closely conform to a suggested NBMR of Root (1989b). However, the data for titmice exceeds the proposed NBMR of 2.45 times BMR and suggests that although a NBMR may exist, the multiple may be higher than 2.45 times BMR.

ACKNOWLEDGMENTS

James Gessaman, Kim Sullivan, Wayne Wurtsbaugh, Walter Koenig, and one anonymous reviewer provided many useful suggestions on earlier drafts of this manuscript. Kim Sullivan generously loaned me the meteorological equipment used in this study. Thanks to Keith Dixon for providing information on study sites and to Jaclyn Cooper and Glenn Wilson for field assistance. This study was supported in part by a North American Bluebird Society student research grant and a Sigma Xi Grant-in-Aid of Research. Birds were captured under federal (#PRT-779300) and state (2COLL1401) scientific collecting permits.

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