

THERMOREGULATION AND HABITAT PREFERENCE IN MOUNTAIN CHICKADEES AND JUNIPER TITMICE

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Abstract. The Mountain Chickadee (*Poecile gambeli*) and the Juniper Titmouse (*Baeolophus ridgwayi*) are closely related, ecologically similar passerines sympatric in portions of their range. However, Mountain Chickadees prefer higher altitude, cooler habitats than Juniper Titmice. We measured oxygen consumption, evaporative water loss, body temperature, and thermal conductance on seasonally acclimatized individuals to determine if thermoregulatory differences correlate with habitat preference. The Mountain Chickadee's lower critical temperature was 4.2°C lower than the Juniper Titmouse's in summer and 2.4°C lower in winter. Thermal conductance decreased significantly in winter relative to summer in Mountain Chickadees but not in Juniper Titmice. The Mountain Chickadee's upper critical temperature was 4.2°C lower than the Juniper Titmouse's in summer. Also in summer, Mountain Chickadees had significantly higher body temperature above the upper critical temperature than Juniper Titmice, indicating less heat tolerance. The overall metabolic response to temperature in these two species suggests that physiology plays a role in maintaining their habitat segregation.

Key words: *Baeolophus ridgwayi*, energy metabolism, evaporative water loss, habitat preference, oxygen consumption, *Poecile gambeli*, thermoregulation.

Termo-regulación y preferencia de hábitat en *Poecile gambeli* y *Baeolophus ridgwayi*

Resumen. Las aves paserinas *Poecile gambeli* y *Baeolophus ridgwayi*, cercanamente emparentadas y ecológicamente similares, se distribuyen de modo simpátrico en partes de sus rangos. Sin embargo, *P. gambeli* prefiere ambientes más elevados y frescos que *B. ridgwayi*. Medimos el consumo de oxígeno, la pérdida de agua por evaporación, la temperatura corporal y la conductancia térmica en individuos aclimatados estacionalmente para determinar si las diferencias en termo-regulación se correlacionan con la preferencia de hábitat. La temperatura crítica menor de *P. gambeli* fue 4.2°C más baja que la de *B. ridgwayi* en el verano y 2.4°C más baja en el invierno. La conductancia térmica disminuyó significativamente en el invierno en relación al verano en *P. gambeli* pero no en *B. ridgwayi*. La temperatura crítica mayor de *P. gambeli* fue 4.2°C más baja que la de *B. ridgwayi* en el verano. También en el verano, *P. gambeli* tuvo una temperatura corporal significativamente mayor, por arriba del límite superior de temperatura crítica, que la de *B. ridgwayi*, indicando menor tolerancia al calor. La respuesta metabólica global a la temperatura en estas dos especies sugiere que la fisiología juega un rol importante en mantener la segregación de sus ambientes.

INTRODUCTION

Climate may influence the biogeography, abundance, and habitat choice of birds physiologically through its impact on energy and water balance, and/or ecologically through its impact on food availability and vegetation (Weathers and van Riper 1982). For birds, the general viewpoint is that climate limits birds through ecological and behavioral factors rather than by physiological factors (Bartholomew 1958, Daw-

son and Bartholomew 1968). However, Root (1988a, 1988b) provided data that indicate the effect of climate on energy expenditure significantly impacts species distribution and abundance. In addition, significant energetic differences are apparent in similar bird species from dissimilar climates which may have an adaptive value (Weathers and van Riper 1982, Hayworth and Weathers 1984, Hinsley et al. 1993, Weathers and Greene 1998).

The Mountain Chickadee (*Poecile gambeli*) and the Juniper Titmouse (*Baeolophus ridgwayi*) are small, mostly nonmigratory members of the Paridae that occupy regions of western North America (Fig. 1). The northern range extent of the Juniper Titmouse may be influenced by daily

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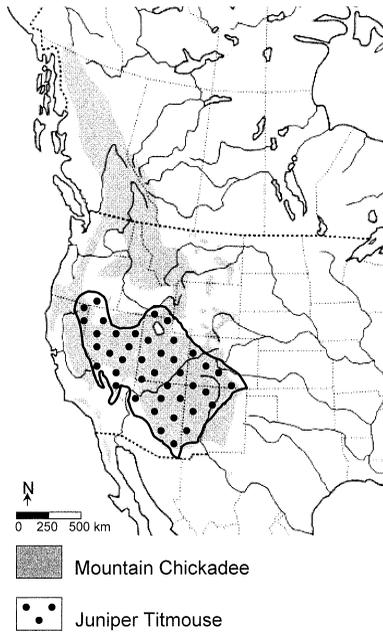


FIGURE 1. Range of Mountain Chickadees and Juniper Titmice (McCallum et al. 1999, Cicero 2000).

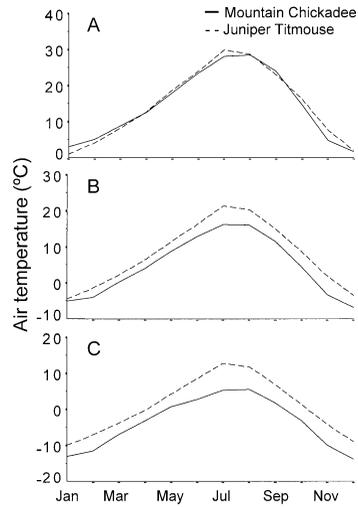


FIGURE 2. Annual temperature profiles for Mountain Chickadee (higher elevation) and Juniper Titmouse (lower elevation) study sites in northern Utah. (A) Mean daily maximum, (B) mean daily, (C) mean daily minimum, plotted for each month. Data are from the Utah Climate Center, Logan, Utah, 1989–1994 (unpubl. data).

energy expenditure especially during winter (Cooper 2000). Throughout their range, Juniper Titmice prefer juniper or mixed pinyon-juniper woodlands with mature junipers that provide cavities for nesting (Cicero 2000). The range of Mountain Chickadees overlaps most of the range of Juniper Titmice. However, chickadees generally prefer pine and spruce-fir habitats (Dixon 1961). Dixon (1961) stated that these two species are separated primarily by altitude in the western United States. Mountain Chickadees prefer elevations of 1800 to 3300 m (Bent 1946) whereas Juniper Titmice prefer lower elevations ranging from around 700 to 2400 m (Cicero 2000). Miller (1946) found that Mountain Chickadees replaced Juniper Titmice above 1980 m in the Grapevine Mountains along the California-Nevada border and attributed these habitat preferences to temperature zonation rather than to vegetation community or structure. For example, patches of pinyon-juniper woodlands above 1980 m were present at this site but were not occupied by Juniper Titmice. In addition, Miller (1946) noted that Mountain Chickadees occurred in several pinyon-juniper woodlands in the western United States but generally not in the warmest locations examined, such as the Kingston Mountains of California.

In the zone of elevational overlap in Utah where both species occupy pinyon-juniper woodlands, Mountain Chickadees prefer moister and cooler habitats than Juniper Titmice (SJC, unpubl. data). For sites in northern Utah where birds were captured for this study, mean daily and mean daily minimum temperatures encountered by the two species vary by as much as 4–5°C seasonally (Fig. 2). In this study, we examine the thermoregulatory abilities of these species in relation to their respective environments.

Two-species comparisons, similar to the present study have been criticized for statistical reasons (Garland and Adolph 1994). However, these studies are important tools in physiological ecology (Weathers and Greene 1998) and the problems pointed out by Garland and Adolph (1994) can be addressed by performing meta-analyses on several two-species comparisons (Gurevitch et al. 1992).

METHODS

Mountain Chickadees were captured in several locations within the Cache National Forest, Cache County, in northeastern Utah (41°52'N, 111°30'W) at elevations of 2180 to 2250 m. Juniper Titmice were captured near Rosette, Box

Elder County, in northwestern Utah (41°50'N, 113°25'W) at an elevation of 1700 m. Mountain Chickadees and Juniper Titmice were captured with mist nets in summer and winter of 1994, 1995, and 1996. Mass at capture was measured to the nearest 0.1 g with an Ohaus model CT-1200 (Pine Brook, New Jersey) portable electronic balance. Following capture, birds were transported to Logan, Utah, where they were housed individually in $0.3 \times 0.3 \times 0.3$ m cages placed in a $3 \times 3 \times 2.5$ m temperature-controlled environmental chamber. The environmental chamber was reprogrammed weekly to simulate the current photocycle and thermal regime of the study site. While in captivity, birds were provided free access to water, grit, and food (*Tenebrio* larvae and wild birdseed). Individuals were tested within 1 week of capture with birds tested from 17 May to 1 September designated "summer birds," and those tested from 20 November to 1 March designated "winter birds." Summer titmice had an initial small decrease (<5%) in mass following capture and then maintained mass in captivity. All other birds maintained mass while caged.

METABOLIC AND EVAPORATIVE WATER LOSS MEASUREMENTS

Nighttime metabolic rate and evaporative water loss were measured for Mountain Chickadees and Juniper Titmice in both summer and winter. 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 (Stamford, Connecticut) 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. Metabolic rate was measured as oxygen consumption ($\dot{V}\text{O}_2$) from 22:00 to 03:00 in summer and from 21:00 to 04:00 (MST) in winter. We fasted birds for at least 4 hr prior to metabolic tests to insure post-absorptive conditions. Individuals were weighed and then placed inside the metabolic chamber where they perched on 1.0-cm wire mesh placed

3.0 cm above a 1-cm layer of paraffin oil used for the collection of fecal material. Oxygen consumption ($\dot{V}\text{O}_2$) was measured using open-circuit respirometry with an Ametek Model S-3A oxygen analyzer (Pittsburgh, Pennsylvania). Dry, CO_2 -free air was drawn through the metabolic chamber using a diaphragm pump. Outlet flow rates of dry, CO_2 -free air were maintained by a Matheson precision rotameter (Model 604, Montgomeryville, Pennsylvania) calibrated to $\pm 1.0\%$ volumetrically (Brooks vol-u-meter, Hatfield, Pennsylvania) and located downstream from the metabolic chamber. These flow rates yielded changes in oxygen content between in-flux and efflux gas of 0.3% to 0.6% and maintained oxygen content of efflux gas above 20.3%. Fractional concentration of oxygen in efflux gas was determined from a 100-mL min^{-1} subsample passed through the oxygen analyzer. This subsample of efflux gas was recorded every 15 sec using Datacan 5.0 data acquisition and analysis program (Sable Systems International, Las Vegas, Nevada). Evaporative water loss was determined over a 60-min timed interval by measuring the increase in mass of a downstream absorbent train containing Drierite (W.A. Hammond Drierite Company, Xenia, Ohio). All weighings were made on an analytical balance (Mettler H51AR, Columbus, Ohio). Weighings were not recorded if any excreta were not completely covered by paraffin oil.

Weathers et al. (1980) found that black paint used to achieve a high wall emissivity in the metabolic chamber was hygroscopic, which leads to errors in evaporative water loss measurements. We determined the degree to which our painted metabolic chambers were hygroscopic by placing a known mass of distilled water in a container in the chambers at a range of temperatures similar to our experiments and measuring the increase in mass of a downstream absorbent train containing Drierite from the evaporation of the water. We used the same flow conditions as in the experiments. The mass loss of the water container was in close agreement of the mass gain in the Drierite absorbent train (SJC, unpubl. data).

$\dot{V}\text{O}_2$ and evaporative water loss were measured on individual birds exposed to a single ambient temperature (T_a) within a temperature range of -10°C to 44°C . The order of temperatures selected was randomized. Each bird was used only once during a 24-hr period and was

tested no more than twice. No individuals were tested twice within any one of the three temperature ranges of interest: below the lower critical temperature, within the thermoneutral zone, or above the upper critical temperature. All individuals were tested within 1 week of capture. At the termination of each metabolic test, birds were removed from the chamber and body temperature (T_b , to the nearest $\pm 0.1^\circ\text{C}$) was recorded 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). The thermocouple was inserted into the cloaca to a depth where further insertion did not alter temperature reading (approximately 10–12 mm). Flow rates were maintained at 442–450 mL min^{-1} for temperatures below 30°C and 1096–1118 mL min^{-1} for temperatures above 30°C . These flow rates maintained chamber dew point temperature below 12°C (Lasiewski et al. 1966). Individual birds were placed in the metabolic chamber for a total of 2 hr for temperatures $\leq 30^\circ\text{C}$. Birds were allowed to equilibrate for the first 60 min and $\dot{V}\text{O}_2$ was measured over the last 60 min of the trial. For metabolic trials above 30°C individuals were placed in the chamber for 60 min. The first 10 min were used for equilibration (time needed for chamber to reach 99% equilibrium using equation of Lasiewski et al. 1966) and $\dot{V}\text{O}_2$ was measured over the last 50 min of the trial. Oxygen consumption was calculated as steady state $\dot{V}\text{O}_2$ using Equation 4a of Withers (1977). All values were corrected for standard temperature and pressure of dry gas. We calculated metabolic heat production assuming 20.087 kJ of heat were produced per liter of oxygen consumed by fasting birds (Gessaman and Nagy 1988).

STATISTICAL ANALYSES

Lower critical temperature (T_{lc}) and upper critical temperature (T_{uc}) were calculated using locally weighted scatterplot smoothing (LOWESS) regression followed by linear regression. The LOWESS technique is useful because it makes no assumptions about the form of the underlying distribution (Cleveland 1985, Bakken et al. 1991). LOWESS was used to determine the approximate T_{lc} and T_{uc} , and then metabolic rates between the two inflection points were pooled and averaged as the basal metabolic rate (BMR). The T_{lc} and T_{uc} were then determined as the in-

tersection of the regression line below and above thermoneutrality, respectively, with a horizontal line through mean BMR for each species and season. Published data for BMR (Cooper 2002), have been included to show the thermoneutral zone for each species in summer and winter. In addition, the BMR data were analyzed for species differences in addition to the seasonal differences reported in Cooper (2002). Data are reported as means \pm SE. We compared means either using independent two-tailed t -tests or covariance analysis (ANCOVA, with body mass as a covariate). Regression lines were fit by the method of least squares. Slopes and intercepts of regression lines were compared using ANCOVA. Statistical significance was accepted at $P < 0.05$. All statistics were computed using SPSS 6.1 (Norusis 1989). Due to the substantial mass differences between species, all values of heat production and evaporative water loss were computed as mass-specific values. In addition, mass-independent values were calculated by dividing rates of heat production and evaporative water loss by body mass raised to the 0.75 power (Kleiber 1947, West et al. 1997, Weathers and Greene 1998). BMR and regression equations of $\dot{V}\text{O}_2$ are also presented on a whole-animal basis because seasonal comparisons may be more effective using per-bird $\dot{V}\text{O}_2$ (Dawson and Smith 1986, Swanson 1991).

RESULTS

BODY MASS

Mean body mass during nocturnal metabolic trials for summer chickadees was 10.8 ± 1.0 g ($n = 29$), which did not differ significantly from the winter chickadee body mass of 11.1 ± 1.0 g ($n = 27$, $t_{54} = -1.1$, $P = 0.28$). Mean body mass of titmice during nocturnal metabolic trials was significantly higher in winter (17.2 ± 1.1 g; $n = 22$ measurements of 16 titmice) compared to summer (16.0 ± 1.0 g; $n = 33$ measurements of 23 titmice; $t_{37} = -4.3$, $P < 0.001$).

METABOLIC RATE

Basal metabolism. BMR was 0.69 ± 0.03 mL O_2 min^{-1} (3.75 ± 0.16 mL O_2 g^{-1} hr^{-1} , $n = 14$) in summer chickadees and 0.81 ± 0.04 mL O_2 min^{-1} (3.01 ± 0.15 mL O_2 g^{-1} hr^{-1} , $n = 16$) in summer titmice. BMR was significantly higher in summer chickadees compared to titmice (ANCOVA: $F_{1,27} = 5.7$, $P = 0.04$). In winter, BMR was 0.81 ± 0.03 mL O_2 min^{-1} (4.36 ± 0.15 mL

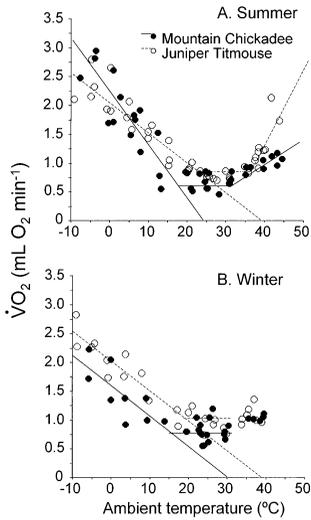


FIGURE 3. Relationship between oxygen consumption ($\dot{V}O_2$) and ambient temperature (T_a) for (A) summer-acclimatized and (B) winter-acclimatized Mountain Chickadees and Juniper Titmice. Horizontal lines represent basal metabolic rate reported in Cooper (2002).

O_2 $g^{-1} hr^{-1}$, $n = 17$) in chickadees and 0.99 ± 0.04 $mL O_2 min^{-1}$ (3.43 ± 0.17 $mL O_2 g^{-1} hr^{-1}$, $n = 12$) in titmice. BMR was significantly higher in winter chickadees compared to titmice (ANCOVA: $F_{1,26} = 9.2$, $P < 0.01$). Intraspecific comparisons show that winter birds had significantly higher BMR compared to summer birds (ANCOVA: chickadees, $F_{1,28} = 5.2$, $P = 0.03$; titmice, $F_{1,25} = 5.0$, $P = 0.03$).

Below thermoneutrality. The summer analyses below T_{lc} yielded the following relationships between $\dot{V}O_2$ and T_a (Fig. 3A) Summer chickadees:

$$\dot{V}O_2 \text{ (mL } O_2 \text{ min}^{-1}\text{)} = 2.20 - 0.091T_a \quad (1)$$

$(n = 15, r^2 = 0.71, P < 0.001).$

Summer titmice:

$$\dot{V}O_2 \text{ (mL } O_2 \text{ min}^{-1}\text{)} = 2.07 - 0.053T_a \quad (2)$$

$(n = 17, r^2 = 0.75, P < 0.001).$

For interspecific comparisons of summer birds below thermoneutrality, the slopes of the two regression lines were significantly different (mass-specific: $F_{1,28} = 24.3$, $P < 0.001$; $mass^{0.75}$: $F_{1,28} = 7.5$, $P < 0.01$) and the intercepts were significantly different (mass-specific: $F_{1,29} = 24.3$, $P < 0.001$; $mass^{0.75}$: $F_{1,29} = 14.2$, $P < 0.01$).

The winter analyses below T_{lc} yielded the following relations (Fig. 3B): Winter chickadees:

$$\dot{V}O_2 \text{ (mL } O_2 \text{ min}^{-1}\text{)} = 1.61 - 0.053T_a \quad (3)$$

$(n = 9, r^2 = 0.58, P < 0.01).$

Winter titmice:

$$\dot{V}O_2 \text{ (mL } O_2 \text{ min}^{-1}\text{)} = 2.03 - 0.053T_a \quad (4)$$

$(n = 10, r^2 = 0.71, P < 0.01).$

Interspecific comparisons of regression equations for winter birds were not significantly different in slopes (mass-specific: $F_{1,15} = 1.3$, $P = 0.27$; $mass^{0.75}$: $F_{1,15} = 0.7$, $P = 0.43$) or intercepts on a $mass^{0.75}$ basis ($F_{1,16} = 2.0$, $P = 0.18$). For chickadees, slopes were significantly different between seasons (mass-specific: $F_{1,20} = 8.0$, $P = 0.02$; $mass^{0.75}$: $F_{1,20} = 7.1$, $P = 0.03$) and intercepts were also significantly different between seasons (mass-specific: $F_{1,21} = 12.1$, $P = 0.002$; $mass^{0.75}$: $F_{1,21} = 11.2$, $P = 0.003$). For titmice, however, neither slopes (mass-specific: $F_{1,23} = 0.0$, $P = 1.0$; $mass^{0.75}$: $F_{1,23} = 0.0$, $P = 1.0$) nor intercepts on a $mass^{0.75}$ basis; $F_{1,24} = 3.2$, $P = 0.09$) were significantly different between seasons. The regression equations relating heat production to T_a below thermoneutrality are in Table 1.

Lower critical temperature (T_{lc}) was calculated as the intersection of the regression line below thermoneutrality with a horizontal line through mean BMR for each species and season, respectively. T_{lc} was $18.7^\circ C$ in summer chickadees, $22.9^\circ C$ in summer titmice, $14.7^\circ C$ in winter chickadees, and $17.1^\circ C$ in winter titmice.

The mean nocturnal T_b within the thermoneutral zone and below the T_{lc} of summer chickadees was $35.5 \pm 1.8^\circ C$ ($n = 18$), which was not significantly different from mean nocturnal T_b of summer titmice ($35.9 \pm 2.6^\circ C$, $n = 24$, $t = -0.5$, $P = 0.60$). The mean nocturnal T_b within the thermoneutral zone and below T_{lc} of winter chickadees was $36.0 \pm 2.2^\circ C$ ($n = 23$), which was not significantly different than mean nocturnal T_b of winter titmice ($35.3 \pm 2.0^\circ C$, $n = 18$, $t = 1.1$, $P = 0.29$).

Above thermoneutrality. The relationship between $\dot{V}O_2$ and T_a above thermoneutrality is shown for summer and winter birds in Figure 3. The summer analyses above T_{uc} yielded the following relations: Summer chickadees:

TABLE 1. Relationship of mass-specific ($m W g^{-1}$) and mass-independent ($m W g^{-0.75}$) heat production to ambient temperature (T_a , °C) outside the thermoneutral zone for seasonally acclimatized Mountain Chickadees and Juniper Titmice from northern Utah.

Species	<i>n</i>	Regression equation ($m W g^{-1}$)	<i>r</i> ²	<i>P</i>	Regression equation ($m W g^{-0.75}$)	<i>r</i> ²	<i>P</i>
Below thermoneutral zone							
Summer							
Chickadee	15	$67.82 - 2.50T_a$	0.65	<0.001	$123.14 - 4.68T_a$	0.67	<0.001
Titmouse	17	$43.94 - 1.19T_a$	0.80	<0.001	$87.50 - 2.33T_a$	0.79	<0.001
Winter							
Chickadee	9	$48.82 - 1.66T_a$	0.71	<0.01	$88.93 - 3.01T_a$	0.68	<0.01
Titmouse	10	$39.49 - 1.19T_a$	0.88	<0.001	$80.42 - 2.34T_a$	0.85	<0.01
Above thermoneutral zone							
Summer							
Chickadee	11	$-11.63 + 1.04T_a$	0.56	<0.01	$-21.35 + 1.88T_a$	0.56	<0.01
Titmouse	9	$-78.76 + 2.66T_a$	0.75	<0.01	$-163.89 + 5.50T_a$	0.73	<0.01

$$\dot{V}O_2 \text{ (mL O}_2 \text{ min}^{-1}\text{)} = -0.39 + 0.034T_a \quad (5)$$

(*n* = 9, *r*² = 0.53, *P* < 0.01).

Summer titmice:

$$\dot{V}O_2 \text{ (mL O}_2 \text{ min}^{-1}\text{)} = -4.40 + 0.144T_a \quad (6)$$

(*n* = 11, *r*² = 0.64, *P* < 0.01).

For interspecific comparisons of summer birds, the slopes of the two regression lines were significantly different (mass-specific: $F_{1,16} = 5.9$, *P* = 0.03; mass^{0.75}: $F_{1,16} = 7.1$, *P* = 0.02) but the intercepts were not significantly different (mass-specific: $F_{1,17} = 2.3$, *P* = 0.15; mass^{0.75}: $F_{1,17} = 0.0$, *P* = 0.89). Interspecific comparisons of regression equations for winter birds were not determined since heat production was not linearly related to ambient temperature above 30°C. However, the winter $\dot{V}O_2$ value above ambient temperature of 35°C was $1.04 \pm 0.04 \text{ mL O}_2$

min^{-1} ($5.76 \pm 0.16 \text{ mL O}_2 \text{ g}^{-1} \text{ hr}^{-1}$, *n* = 5) in chickadees and $1.08 \pm 0.18 \text{ mL O}_2 \text{ min}^{-1}$ ($3.96 \pm 0.16 \text{ mL O}_2 \text{ g}^{-1} \text{ hr}^{-1}$, *n* = 5) in titmice. $\dot{V}O_2$ above 35°C was significantly higher in winter chickadees compared to titmice (ANCOVA: $F_{1,7} = 17.9$, *P* < 0.01). The regression equations relating heat production to T_a above thermoneutrality are in Table 1.

Upper critical temperature (T_{uc}) in summer birds was calculated as the intersection of the regression line above thermoneutrality with a horizontal line through mean BMR for each species, respectively. T_{uc} was 31.5°C in summer chickadees and 35.7°C in summer titmice. T_{uc} for winter chickadees and titmice could only be estimated with LOWESS regression since metabolism above thermoneutrality was not a linear function of T_a (Fig. 3B). T_{uc} was approximately 32°C for winter chickadees and 34°C for winter titmice.

The pooled body temperatures for chickadees and titmice in summer and winter increased linearly with increasing ambient temperature above 35°C (Fig. 4). The pooled data above 35°C yielded the following relationship:

$$T_b(\text{°C}) = 26.30 + 0.39T_a \quad (7)$$

(*n* = 30, *r*² = 0.43, *P* < 0.01).

Mean body temperature above T_{uc} in summer chickadees was $42.9 \pm 0.6^\circ\text{C}$ (*n* = 11), which was significantly higher than summer titmice ($41.4 \pm 0.3^\circ\text{C}$, *n* = 9; *t* = 2.2, *P* = 0.04). Mean body temperature above 35°C in winter chicka-

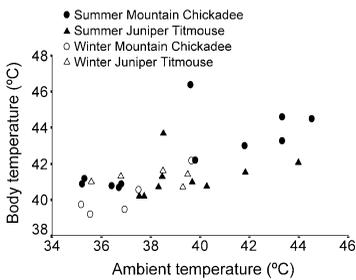


FIGURE 4. Relationship between body temperature (T_b) and ambient temperature (T_a) above 35°C for Mountain Chickadees and Juniper Titmice in summer and winter.

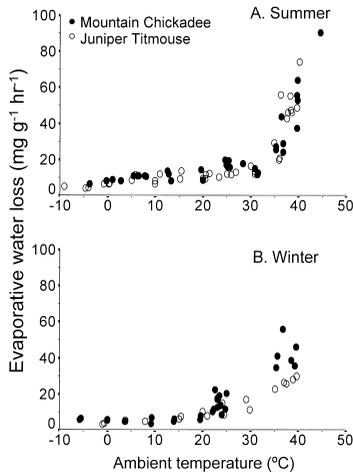


FIGURE 5. Relationship between evaporative water loss and ambient temperature (T_a) for (A) summer-acclimatized and (B) winter-acclimatized Mountain Chickadees and Juniper Titmice.

dees was $41.2 \pm 0.2^\circ\text{C}$ ($n = 5$), which was not significantly different than winter titmice ($41.2 \pm 0.5^\circ\text{C}$, $n = 5$; $t = 1.8$, $P = 0.12$).

EVAPORATIVE WATER LOSS

In summer, above 30°C the rate of evaporative water loss of both species increased exponentially (Fig. 5A), as is typical of endotherms. In winter, above 20°C the rate of evaporative water loss of both species increased exponentially (Fig. 5B). In order to compare the evaporative water loss response to varying temperature, the log EWL versus T_a for both species was determined. The summer analyses of the relationship between log EWL and T_a yielded the following relations: Summer chickadees:

$$\log \text{EWL (mg g}^{-1} \text{ hr}^{-1}) = 0.846 + 0.018T_a \quad (8)$$

$$(n = 33, r^2 = 0.73, P < 0.001).$$

Summer titmice:

$$\log \text{EWL (mg g}^{-1} \text{ hr}^{-1}) = 0.745 + 0.020T_a \quad (9)$$

$$(n = 35, r^2 = 0.78, P < 0.001).$$

For interspecific comparisons of summer birds, the slopes of the two regression lines were not significantly different (mass-specific: $F_{1,64} = 1.0$, $P = 0.33$; $\text{mass}^{0.75}$: $F_{1,64} = 0.1$, $P = 0.34$) and the intercepts were not significantly differ-

ent (mass-specific: $F_{1,65} = 1.3$, $P = 0.25$; $\text{mass}^{0.75}$: $F_{1,65} = 0.0$, $P = 0.98$).

The winter analyses of the relationship between log EWL and T_a yielded the following relations: Winter chickadees:

$$\log \text{EWL (mg g}^{-1} \text{ hr}^{-1}) = 0.645 + 0.022T_a \quad (10)$$

$$(n = 30, r^2 = 0.76, P < 0.001).$$

Winter titmice:

$$\log \text{EWL (mg g}^{-1} \text{ hr}^{-1}) = 0.540 + 0.022T_a \quad (11)$$

$$(n = 17, r^2 = 0.94, P < 0.001).$$

Interspecific comparisons of regression equations for winter birds were not significantly different in slopes (mass-specific: $F_{1,43} = 0.0$, $P = 0.94$; $\text{mass}^{0.75}$: $F_{1,43} = 0.0$, $P = 0.86$). The intercepts were significantly different on a mass-specific basis ($F_{1,44} = 6.4$, $P = 0.02$) but not on a $\text{mass}^{0.75}$ basis ($F_{1,44} = 2.0$, $P = 0.17$). For chickadees, slopes were significantly different between seasons (mass-specific: $F_{1,59} = 2.9$, $P = 0.03$; $\text{mass}^{0.75}$: $F_{1,59} = 2.7$, $P = 0.03$) and so were intercepts (mass-specific: $F_{1,60} = 5.0$, $P = 0.03$; $\text{mass}^{0.75}$: $F_{1,60} = 4.9$, $P = 0.03$). For titmice, slopes were not significantly different between seasons (mass-specific: $F_{1,48} = 0.6$, $P = 0.46$; $\text{mass}^{0.75}$: $F_{1,48} = 0.4$, $P = 0.54$) but intercepts were (mass-specific: $F_{1,49} = 13.4$, $P < 0.01$; $\text{mass}^{0.75}$: $F_{1,49} = 11.9$, $P < 0.01$).

THERMAL CONDUCTANCE

Overall thermal conductance below thermoneutrality is equivalent to the slope of the line relating $\dot{V}\text{O}_2$ to ambient temperature only if the curve extrapolates to T_b at zero metabolism. Since the metabolic data from chickadees and titmice did not conform to the Newton-Scholander cooling model (Scholander et al. 1950) we calculated overall thermal conductance (K_{es}) for individuals using the equation of Bakken (1976)

$$K_{es} = (M - E)/(T_b - T_a) \quad (12)$$

where M is metabolic rate and E is evaporative heat loss (assuming 2.43 J of heat for each mg of water evaporated). Thermal conductance below thermoneutrality was $1.57 \pm 0.13 \text{ mW g}^{-1} \text{ }^\circ\text{C}^{-1}$ for summer chickadees ($n = 15$), which was significantly higher than $1.02 \pm 0.07 \text{ mW g}^{-1} \text{ }^\circ\text{C}^{-1}$ for summer titmice ($n = 17$, $t = 3.9$, $P < 0.01$). Thermal conductance for winter chickadees was $1.21 \pm 0.09 \text{ mW g}^{-1} \text{ }^\circ\text{C}^{-1}$ ($n = 9$),

which was not significantly different from winter titmice ($1.10 \pm 0.03 \text{ mW g}^{-1} \text{ }^\circ\text{C}^{-1}$, $n = 10$, $t = 1.6$, $P = 0.14$). Thermal conductance was not significantly different between summer and winter titmice ($t = 1.1$, $P = 0.28$) but was significantly lower in winter chickadees compared to summer ($t = -2.2$, $P = 0.04$).

DISCUSSION

METABOLIC RESPONSE TO TEMPERATURE BELOW THERMONEUTRALITY

Lower critical temperature in both species varied with acclimatization state and was lowest in winter. The Mountain Chickadee's T_{lc} was 4.2°C lower in summer and 2.4°C lower in winter than the Juniper Titmouse's. In addition, the T_{lc} for Mountain Chickadees was 2.2°C and 6.4°C lower than predicted values based on body mass (Weathers and van Riper 1982) for summer and winter, respectively. The T_{lc} for Juniper Titmice was 3.4°C higher in summer and only 1.3°C lower than predicted values based on body mass (Weathers and van Riper 1982). The slope and intercept of the regression line relating metabolic rate to ambient temperature below thermoneutrality varied seasonally in chickadees but not in titmice. This suggests that chickadees have better insulation in winter, probably as result of increased plumage mass, but increased plumage mass in titmice does not increase insulation (Cooper 2002). Minimal dry thermal conductance below thermoneutrality also decreased significantly in winter chickadees but not in titmice. Overall insulative capacity in summer is greater in titmice than in chickadees but in winter is not significantly different between the two species based on values of overall minimum thermal conductance. This suggests that seasonal changes in insulation are involved with winter acclimatization of the Mountain Chickadee but not of the Juniper Titmouse. However, winter values of thermal conductance exceeded those allometrically predicted for passerines (Aschoff 1981) by 26% for titmice and 13% for chickadees indicating that insulative changes are probably not prominently involved with winter acclimatization in these two species.

METABOLIC RESPONSE TO TEMPERATURE ABOVE THERMONEUTRALITY

Mountain Chickadees appear to be markedly heat intolerant. The T_{uc} for summer chickadees was only 31.5°C , which is one of the lowest re-

ported for birds (Weathers 1981, Weathers and van Riper 1982, Hayworth and Weathers 1984). For Juniper Titmice in northern Utah (this study), a T_{uc} of 35.7°C in summer is also lower than several other passerines (see Weathers 1981). In comparison, Juniper Titmice from southeastern Arizona have a T_{uc} between 38°C and 40°C (Weathers and Greene 1998). Given the very low T_{uc} of summer chickadees it is surprising that the slope relating $\dot{V}\text{O}_2$ to T_a was actually less steep than titmice. This slope is referred to as the coefficient of heat strain (Weathers 1981) with steeper slopes reflecting lower heat tolerance. The coefficient of heat strain for summer chickadees is only 40% of the allometric prediction, while the coefficient of heat strain for summer titmice is 129% of the predicted value (Weathers 1981). The low coefficient of heat strain for summer chickadees is very similar to values reported for Bridled Titmice (69% of predicted) and Juniper Titmice (50% of predicted) from southeastern Arizona (Weathers and Greene 1998).

In spite of their low coefficient of heat strain in summer, T_b above the T_{uc} for Mountain Chickadees was significantly higher than Juniper Titmice. Body temperature above the T_{uc} averaged 5.1°C higher than within the thermoneutral zone for summer chickadees but only 3.0°C for summer titmice. Increased levels of hyperthermia permit chickadees to lose more heat by non-evaporative pathways than titmice (Weathers 1981). However, in spite of hyperthermia, chickadees did not have any reduction in evaporative water loss compared to titmice above T_{uc} indicating more heat stress in chickadees above T_{uc} compared to titmice. In addition, $\dot{V}\text{O}_2$ above 35°C was significantly higher in winter chickadees compared to winter titmice. Similar heat intolerance has been found in three Hawaiian honeycreepers, the Palila (*Loxioides bailleui*; Weathers and van Riper 1982) and the Hawai'i and Kauai 'Amakihi, (*Hemignathus virens* and *H. kauaiensis*; MacMillen 1974), which are restricted to cool, high forests or montane habitats.

EVAPORATIVE WATER LOSS

Evaporative water loss was not different between summer chickadees and titmice. Both species had relatively high rates of evaporative water loss. For example, for summer birds evaporative water loss above T_{uc} was approximately $2.0\times$ higher in birds from this study compared

to Juniper Titmice from southeastern Arizona (Weathers and Greene 1998). Whether this decreased evaporative water loss in southern populations that inhabit warmer, drier climates is a common feature of the avian thermoregulatory response to heat is uncertain. In winter, titmice had lower evaporative water loss than chickadees on a mass-specific basis but not on a mass-independent basis. Winter titmice and chickadees had lower evaporative water loss over the entire range of temperatures tested compared to their summer counterparts. It is possible that cutaneous water loss decreases in winter because increased plumage mass retards water-vapor diffusion. However, for small birds, the total resistance of plumage and the boundary layer of still air around the bird is generally quite low (Webster et al. 1985).

Mountain Chickadees have greater cold tolerance than Juniper Titmice as demonstrated by a decreased lower critical temperature in both summer and winter and seasonal changes in thermal conductance. This could be advantageous for chickadees that inhabit higher altitudes since climate may be more unpredictable than lower sites occupied by titmice. In addition, chickadees have significantly higher maximum thermogenic capacity than titmice in both summer and winter (Cooper 2002). On the other hand, Juniper Titmice appear to be better able to tolerate higher temperatures than Mountain Chickadees. Summer titmice have a higher upper critical temperature than summer chickadees and also have lower body temperature under heat stress. Thus, the overall metabolic response to temperature in these two species appears to play a role in maintaining their habitat preferences.

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