

NOCTURNAL HYPOTHERMIA IN SEASONALLY ACCLIMATIZED MOUNTAIN CHICKADEES AND JUNIPER TITMICE

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Abstract. We measured body temperature of Mountain Chickadees (*Poecile gambeli*) and Juniper Titmice (*Baeolophus ridgwayi*) at different times of day and under a range of ambient temperatures in order to determine the use of nocturnal hypothermia in seasonally acclimatized small passerines. Our findings show both species used nocturnal hypothermia year-round. Depth of hypothermia was inversely correlated to body mass in Juniper Titmice but not in Mountain Chickadees. In both species, depth of hypothermia did not vary seasonally but nocturnal body temperature was regulated 3–11°C lower than daytime values. Nocturnal energy savings range from 7%–50% in chickadees and from 10%–28% in titmice. These nocturnal energy savings translate into ecologically important reductions in daily energy expenditures for these two species.

Key words: *Baeolophus ridgwayi*, body temperature, energy metabolism, nocturnal hypothermia, *Poecile gambeli*.

Hipotermia Nocturna en Individuos de *Poecile gambeli* y *Baeolophus ridgwayi* Aclimatados Estacionalmente

Resumen. Medimos la temperatura corporal de *Poecile gambeli* y *Baeolophus ridgwayi* a diferentes horas del día y en un rango de temperaturas ambientales para determinar el uso de hipotermia nocturna en pequeñas aves paserinas aclimatadas estacionalmente. Nuestros resultados muestran que ambas especies presentaron hipotermia nocturna durante todo el año. La profundidad de la hipotermia estuvo inversamente correlacionada con la masa corporal en *B. ridgwayi*, pero no en *P. gambeli*. En ambas especies, la profundidad de la hipotermia no varió estacionalmente, pero la temperatura corporal nocturna estuvo regulada 3–11°C por debajo de los valores diurnos. El ahorro nocturno de energía varió entre 7%–50% en *P. gambeli* y entre 10%–28% en *B. ridgwayi*. Estos ahorros nocturnos de energía se tradujeron en reducciones ecológicamente importantes en los gastos diarios de energía para ambas especies.

Species that overwinter in cold climates endure periods of potentially high energetic demands, especially for small birds that live at high latitudes or altitudes (Bryant and Tatner 1988, Weathers et al. 1999, Cooper 2000, Webster and Weathers 2000, Doherty et al. 2001). Birds that overwinter in cold temperate regions must maintain high metabolic rates in order to maintain normothermic body temperatures during times of extreme cold, shorter daylength, and possible decreased access to food due to snow or ice cover. However, during the nocturnal roost, facultative hypothermia may be used to save energy and decrease foraging needs (McKechnie and Lovegrove 2002).

Hypothermia is defined as any core body temperature (T_b) below the setpoint specified for the active state of the species. For birds, hypothermia generally occurs nocturnally and has traditionally been defined as a decrease in T_b to 30–38°C (Reinertsen 1996); a reduction from the mean of 41.6°C for the active phase of most songbirds (Prinzinger et al. 1991). Nocturnal hypothermia has been documented for several passerine species in the family Paridae, such as Black-capped Chickadees (*Poecile atricapilla*), Carolina Chickadees (*P. carolinensis*), Gray-headed Chickadees (*P. cincta*), and Willow Tits (*P. montana*, Steen 1958, Haftorn 1972, Chaplin 1976, Mayer et al. 1982, Reinertsen and Haftorn 1983). For these species, a reduction in T_b of 4–10°C resulted in savings of 10%–33% in overnight energy expenditure. However, general patterns of hypothermia in parids are not consistent. For example, Black-capped Chickadee, living in Alaska near the northern range boundary had nocturnal T_b only 3°C below daytime T_b (Grossman and West 1977). However, Sharbaugh (2001) recorded an average reduction in T_b of 4–10°C in Black-capped Chickadees from Alaska that were exposed to cold temperature in both summer and winter. In contrast to Black-capped Chickadees, depth of hypothermia varied seasonally in Willow Tits (Reinertsen and Haftorn 1983) where winter birds had lower hypothermic T_b s than their summer counterparts. In addition, Reinertsen and Haftorn (1986) found that Great Tits (*Parus major*) did not utilize nocturnal hypothermia unless they had below-normal energy reserves when entering the roost.

We measured T_b over a wide range of ambient temperatures in seasonally acclimatized Mountain Chickadees (*Poecile gambeli*) and Juniper Titmice (*Baeolophus ridgwayi*). Mountain Chickadees and Juniper Titmice are small, mostly nonmigratory members of the Paridae family that occupy coniferous forests of west-

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ern North America. They inhabit relatively high altitude regions (~700–3300 m; Bent 1946) characterized by harsh climatic conditions throughout much of the year. Thus, they may use hypothermia to a greater extent than parids from low altitudes.

METHODS

Mountain Chickadees and Juniper Titmice were captured in Box Elder and Cache County, Utah, (1700–2250 m altitude) in mist nets in summer and winter of 1994 to 1996. Body mass was measured upon capture to the nearest 0.1 g with a portable electronic balance (Ohaus CT-1200, Pine Brook, New Jersey). Following capture, birds were transported to the laboratory where they were housed individually in cages (30 × 25 × 30 cm) placed inside a temperature-controlled environmental chamber (3 × 3 × 2.5 m). The environmental chamber and photoperiod followed a daily cycle that approximated the season and study site to which the bird had been accustomed. While in captivity, birds were provided free access to water, grit, and food (*Tenebrio* larvae and sunflower seeds). All individual birds maintained mass while in captivity. Individuals were tested within 1 week of capture. Birds tested from 11 May to 30 August were designated “summer birds,” and those tested from 25 November to 1 March were designated “winter birds.”

BODY TEMPERATURE MEASUREMENTS

All T_b measurements were taken using a 30-gauge copper-constantan thermocouple attached to an Omega thermometer (Model HH25-TC, Stamford, Connecticut). The thermocouples were calibrated to a mercury 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). Body temperature was recorded immediately upon capture and after daytime and nighttime metabolic measurements.

METABOLIC RATE MEASUREMENTS

Details on the measurement of metabolic rate at ambient temperatures (ranging from –10 to 30°C) are reported in Cooper (2000), and Cooper and Gessaman (2004). Briefly, birds were placed into a metabolic chamber constructed from a 3.8-L paint can. The inside of the can was painted flat black to provide an emissivity near 1.0. Birds rested on hardware cloth above paraffin oil that was used to collect excreta. Rates of oxygen consumption ($\dot{V}O_2$) were measured continuously using open-circuit respirometry with an Ametek S-3A oxygen analyzer (Pittsburgh, Pennsylvania). Dry, CO₂-free air was drawn through the metabolic chamber using a diaphragm pump. Outlet flow rates of dry, CO₂-free air were maintained at 452–460 mL min⁻¹ which yielded changes in oxygen content between influx and efflux gas of 0.3% and 0.6% and maintained oxygen content of efflux gas above 20.3%. Measurements of outlet gas concentrations were recorded every 15 sec on a computer using Datacan 5.0 data collection and analysis software (Sable Systems International, Las Vegas, Nevada). $\dot{V}O_2$ was measured on individual birds exposed to a single temperature within the series for two hours. The first hour was used to let the bird equilibrate and $\dot{V}O_2$ was measured over

the last hour of the trial. Oxygen consumption was calculated as steady state $\dot{V}O_2$ using equation 4a of Withers (1977). All values were corrected to standard temperature and pressure.

Nocturnal energy savings due to hypothermia for chickadees and titmice was determined as the difference between the predicted $\dot{V}O_2$ of normothermic individuals and the measured $\dot{V}O_2$ of hypothermic individuals. Predicted normothermic $\dot{V}O_2$ was calculated at 10°C intervals over the T_a range of –10 to 20°C using the equation $\dot{V}O_2 = C(T_b - T_a)$, where C is thermal conductance. Minimal thermal conductance values for chickadees and titmice from Cooper (1998) were used at each temperature interval and we used an average resting phase T_b of 39°C (Prinzinger et al. 1991) to calculate normothermic $\dot{V}O_2$.

STATISTICAL ANALYSES

All data are presented as mean ± SD. Means of T_b were compared using Student's t -tests as variances were not significantly different and data met the assumptions of normality. Least-squares linear regression was used to evaluate the relationship between ambient and body temperature. The effect of body reserves on depth of hypothermia in seasonally acclimatized individuals was determined by a multiple regression of body mass and T_a on T_b . All statistics were computed using SPSS 6.1 (Norusis 1989) and we report statistical significance at $P < 0.05$.

RESULTS

Mean body mass ranged from 10.8–11.4 g ($n = 100$) in chickadees and from 16.0–17.2 g ($n = 45$) in titmice depending upon season and time of day (Cooper 1998).

Mean daytime T_b of chickadees was $39.2 \pm 1.6^\circ\text{C}$ in summer (range = 38.0–43.0°C, $n = 50$) and did not significantly differ from daytime T_b of winter chickadees ($38.9 \pm 1.2^\circ\text{C}$, range = 38.0–42.6°C, $n = 42$, $t_{90} = 1.0$, $P = 0.30$). Mean daytime T_b of titmice was $39.8 \pm 1.6^\circ\text{C}$ in summer (range = 38.5–41.7°C, $n = 21$) and did not differ significantly from daytime T_b of winter titmice ($39.5 \pm 1.1^\circ\text{C}$, range = 38.0–41.6°C, $n = 16$, $t_{35} = 0.7$, $P = 0.47$). Nocturnal T_b of chickadees in summer ($35.5 \pm 1.8^\circ\text{C}$, range = 31.5–37.6°C, $n = 18$) did not significantly differ from nocturnal T_b of winter chickadees ($36.0 \pm 2.2^\circ\text{C}$, range = 31.1–38.8°C, $n = 23$, $t_{39} = -0.9$, $P = 0.39$). There was no significant difference ($t_{40} = 0.7$, $P = 0.47$) in nocturnal T_b of titmice in summer ($35.8 \pm 2.6^\circ\text{C}$, range = 28.3–38.6°C, $n = 24$) or winter ($35.3 \pm 2.0^\circ\text{C}$, range = 31.2–38.8°C, $n = 18$, Fig. 1). However, in summer and winter, mean nocturnal T_b was significantly lower than mean daytime T_b (summer chickadees; $t_{66} = -7.7$, $P \leq 0.001$, summer titmice; $t_{43} = -6.6$, $P \leq 0.001$, winter chickadees; $t_{63} = -7.0$, $P \leq 0.001$, winter titmice; $t_{52} = -7.6$, $P \leq 0.001$) indicating that regardless of season, chickadees and titmice use nocturnal hypothermia as a strategy to save energy. Since continuous T_b measurements for individuals were not recorded, the exact duration of the hypothermic period is unknown. The duration of the hypothermic period was estimated by visual inspection of a quadratic fit of time on T_b . The duration of the hypothermic period was calculated as the time period in which the average T_b was below

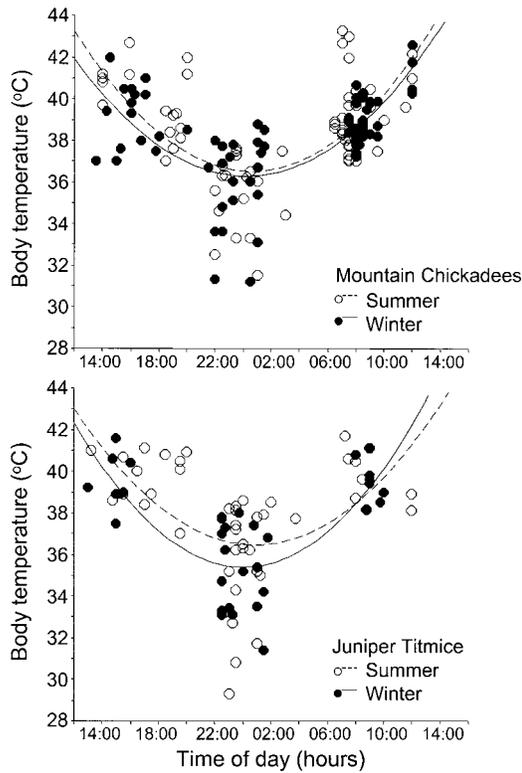


FIGURE 1. Daily body temperature rhythm of summer and winter-acclimatized Mountain Chickadees and Juniper Titmice from northern Utah. Lines represent a quadratic fit of the data. Sample sizes are as follows: summer chickadees, day, $n = 50$ and night, $n = 18$; winter chickadees, day, $n = 42$; night, $n = 23$; summer titmice, day, $n = 21$ and night, $n = 24$; winter titmice, day, $n = 16$ and night, $n = 18$.

38°C. Nocturnal hypothermia was used by both species for approximately a 9 to 10-hr period in summer and a 14-hr period in winter (Fig. 1).

Depth of hypothermia in seasonally acclimatized birds exposed to temperatures below their lower critical temperature varied with T_a in titmice (Fig. 2) but not chickadees (summer chickadees; $n = 15$, $r^2 < 0.001$, $P = 0.95$, winter chickadees; $n = 10$, $r^2 = 0.20$, $P = 0.20$). Body mass did not contribute to depth of hypothermia in chickadees (summer; $n = 15$, $P = 0.23$, winter $n = 10$, $P = 0.08$) but body mass and T_a were significantly correlated with T_b in titmice (summer; $n = 18$, $r^2 = 0.79$, $P < 0.001$, winter; $n = 10$, $r^2 = 0.82$, $P < 0.001$).

Nocturnal energy savings, the percent reduction in metabolism for hypothermic birds compared to predicted metabolism for normothermic individuals, ranged from 7%–50% in chickadees and from 10%–28% in titmice (Table 1). The decreased energy savings with associated decreased T_a were more pronounced in chickadees compared to titmice.

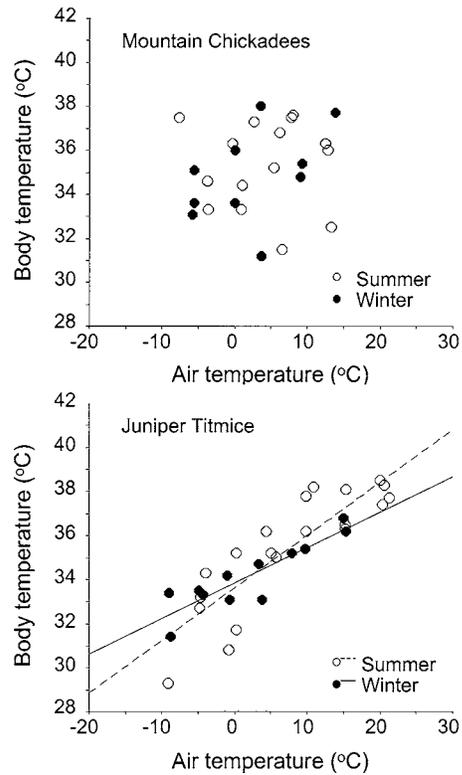


FIGURE 2. The relationship between nocturnal body temperature and ambient temperature below the lower critical temperature for summer and winter-acclimatized Mountain Chickadees and Juniper Titmice from northern Utah. Linear regression equations for summer titmice: $T_b = 33.67 \pm 0.22 T_a$ ($n = 18$, $r^2 = 0.67$, $P < 0.001$), and winter titmice: $T_b = 33.84 \pm 0.16 T_a$ ($n = 12$, $r^2 = 0.80$, $P < 0.001$).

TABLE 1. Calculated energy savings associated with nocturnal hypothermia in summer and winter-acclimatized Mountain Chickadees and Juniper Titmice. Energy savings are the percent reduction in metabolism in hypothermic birds compared to predicted normothermic rates.

Temperature (°C)	Summer Energy Savings (%)		Winter Energy Savings (%)	
	Chickadees	Titmice	Chickadees	Titmice
20	49.8	16.0	39.7	27.8
10	20.1	13.5	17.4	18.2
0	8.9	12.3	12.1	13.6
-10	7.1	11.5	12.4	9.7

DISCUSSION

Mountain Chickadees and Juniper Titmice use nocturnal hypothermia throughout the annual cycle. In summer birds, nocturnal T_b decreased 4–11°C below mean daytime T_b in each species. In winter, nocturnal T_b decreased 3–9°C below mean daytime T_b in each species. There were no seasonal differences in mean daytime or mean nocturnal T_b for either species. This contrasts with Black-capped Chickadees from New York (Chaplin 1974) and Willow Tits (Reinertsen and Haftorn 1983) that have significantly lower nocturnal T_b in winter relative to other seasons. The lack of seasonal change in depth of hypothermia may be in part due to the high climatic variability associated with high altitude. Gray-crowned Rosy-finches (*Leucosticte tephrocotis*) captured in the White Mountains of California (2500 to 4200 m elevation) also lack seasonal differences in T_b during nocturnal hypothermia (Clemens 1989).

Although depth of hypothermia was not related to season, degree of hypothermia below the thermoneutral zone was dependent on T_a in titmice. A similar relationship was found for Gray-headed Chickadees (Haftorn 1972), Black-capped Chickadees (Chaplin 1976), and Willow Tits (Reinertsen and Haftorn 1983). For Mountain Chickadees, the lack of association between T_b and T_a may allow them to save energy by using hypothermia at relatively high temperatures during the summer.

In addition to T_a , the amount of body reserves appears to be an important factor in regulating depth of hypothermia. In titmice, T_b was dependent on the combined effects of T_a and body mass. Thus, birds with lower energy reserves entering the roost at night decreased T_b more than a bird with greater reserves. The relationship between degree of hypothermia and body reserves has also been found in Great Tits, Common Redpolls (*Carduelis flammea*) and Willow Tits (Reinertsen and Haftorn 1983, 1986). Among chickadees, body mass was not related to depth of hypothermia in summer or winter. Since we did not restrict food resources in this study, one explanation may be that chickadees exhibit this pattern only when energy reserves are depleted. However, Hester (1996) also found that overnight resting metabolic rates and T_b s were not dependent on energy stores in winter-acclimatized Black-capped Chickadees. The lack of association between T_b and body mass may provide significant energetic savings for mountain chickadees even when foraging is not restricted.

We calculated nocturnal energy savings to show a difference in energy savings across a range of temperatures. It should be pointed out that energy savings are not constant. T_a affects T_b in titmice and thermal conductance varies with T_a in summer-acclimatized chickadees (Cooper 1998). In addition, as T_a decreases below the lower critical temperature, overall metabolism increases due to increased thermoregulatory costs. Thus, the percent energy savings declines with decreasing T_a .

Nocturnal hypothermia and the associated savings in energy can translate into ecologically important reduced daily energy expenditure. These daily energy expenditures can be calculated to show the importance

of nocturnal hypothermia as an energy saving strategy (Cooper 2000). For example, a 9-hr summer evening at 10°C would result in an energy conservation of 4.75 kJ for chickadees and 4.34 kJ for titmice. These totals represent a 9.7% reduction in daily energy expenditure for chickadees and 9.0% reduction for titmice. In winter, chickadees would conserve 9.08 kJ and titmice would conserve 7.27 kJ during a 14-hr evening at -10°C. This results in chickadees reducing daily energy expenditure by 13.7% while titmice would reduce daily energy expenditure by 7.4%. These energy reductions may be critical to the survival of individuals especially during inclement winter weather.

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EVALUATION OF ALLOZYME AND MICROSATELLITE VARIATION IN TEXAS AND FLORIDA MOTTLED DUCKS

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Abstract. Genetic variation was evaluated in Florida Mottled Ducks (*Anas fulvigula*), and Mottled Ducks from the larger Texas population using 22 allozyme and 5 microsatellite loci. Both marker types revealed differences in allele frequencies between populations and each population possessed rare and unique alleles. Overall allelic distributions were significantly different between the two populations, primarily due

to significant differences at three allozyme and four microsatellite loci. Significant genetic differentiation was revealed between populations with both marker types, however, over all loci, only 5–6% of the variation detected was partitioned between populations. The Florida population possessed lower levels of allozyme heterozygosity and allelic diversity than the Texas population. In contrast, microsatellite heterozygosities and allelic diversity were similar between populations. These data indicate that there is limited gene flow between populations, suggesting that populations should continue to be managed separately.

Key words: *allozyme, Anas fulvigula, microsatellite, Mottled Duck.*

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