

## THE THERMAL AND ENERGETIC SIGNIFICANCE OF CAVITY ROOSTING IN MOUNTAIN CHICKADEES AND JUNIPER TITMICE<sup>1</sup>

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**Abstract.** I examined the thermal and energetic benefits of cavity roosting in summer and winter-acclimatized Mountain Chickadees (*Poecile gambeli*) and Juniper Titmice (*Baeolophus griseus*). Reduction of wind speed inside the cavity increased standard operative temperature 2.5 to 5.9°C compared to the open sites in summer and 12.1 to 14.7°C in winter. Nocturnal energy savings ranged from 23.8 to 27.9% for summer birds and 25.1 to 37.6% for winter birds roosting in cavities. Wind speed was significantly lower inside cavities compared to open sites. These energy savings result in increased fasting endurance of 2.2 to 3 hr in summer and 5.7 to 7.3 hr in winter, which may be critically important for survival throughout the annual cycle for these two species.

**Key words:** *Baeolophus griseus*, *cavity roosting*, *energy metabolism*, *Juniper Titmouse*, *Mountain Chickadee*, *Poecile gambeli*, *thermal microclimate*.

Roost-site selection by small birds can minimize thermoregulatory stress during the overnight fast. Factors that might be important in roost-site selection include local air temperature, shelter from wind and precipitation, and radiation balance (Walsberg 1986). Studies of roost-site selection by small birds in winter has received considerable attention because harsh climatic conditions and short daylength potentially threaten energy balance in winter-acclimatized individuals (Mayer et al. 1982, Buttemer 1985). However, because basal and thermoregulatory costs typically account for 40–60% of total daily energy expenditure in birds (Walsberg 1983), roost-site selection and the resulting microclimate may be important in the ecological energetics of small birds throughout the annual cycle.

In order to determine the possible year-round importance of nocturnal roost-site selection on the energy balance of small birds, I examined micrometeorological variables at the roost in both summer and winter for two small passerine species, the Mountain Chickadee (*Poecile gambeli*) and the Juniper Titmouse (*Baeolophus griseus*), which are year-round residents of coniferous forests in western North America. Both species use natural and artificial cavities as nocturnal roost sites (Bent 1946). These two species are good models for a seasonal study of roost-site selection be-

cause they inhabit relatively high altitude habitats characterized by harsh climatic conditions nearly year-round.

### METHODS

#### STUDY AREA

Mountain Chickadee roost sites were studied within the Cache National Forest, Cache County, in northeastern Utah (41°52'N, 111°34'W) at an elevation of 2,200 m. Juniper Titmouse roost sites were studied in the Raft River Mountains, near Rosette, Box Elder County, in northwestern Utah (41°50'N, 113°25'W) at an elevation of 1,700 m. Mean minimum air temperature in February for each study site is -11.6°C for Mountain Chickadees and -7.1°C for Juniper Titmice. For July, the mean minimum air temperatures are 5.1°C and 12.8°C at the chickadee and titmouse sites, respectively (Utah Climate Center, Logan, Utah).

#### CAVITY ROOSTS

In April 1994, I placed a total of 12 nest boxes (15 × 15 × 25 cm, 32-mm entrance hole) in both study areas. During December 1995, I removed four boxes that had been used by either chickadees or titmice. For microclimate sampling, I attached each of these four nest boxes separately on an adjustable 19-mm diameter metal pole. The nest boxes were placed at a height of 1.5 m with the back of the box touching the trunk of a known roost site. Known roost sites were locations from which a nest box had been removed. The four nest boxes were oriented so that each one faced a different compass direction from the trunk of a single tree.

#### MICROCLIMATE SAMPLING

Microclimate data were collected at 15-min intervals and averaged over 2-hr periods by an electronic data logger (Model CR10, Campbell Scientific, Inc., Logan, Utah). Microclimate data were recorded from the four nest boxes (cavities) and from two sets of instruments placed 3-m away from the nearest nest box in the open. Microclimate sensors in the open were at the same height as the nest boxes. Microclimate variables measured in the open were: (1) air temperature ( $T_a$ ) (shaded 36-gauge copper-constantan thermocouple), (2) operative temperature ( $T_o$ ) (3.5-cm diameter copper sphere thermometer painted flat gray; Bakken et al. 1985, Walsberg and Weathers 1986), and wind speed ( $u$ ) (Thornwaite model 901 cup anemometer). In order to evaluate possible metabolic heating of the air inside the cavity, I placed a single Mountain Chickadee or

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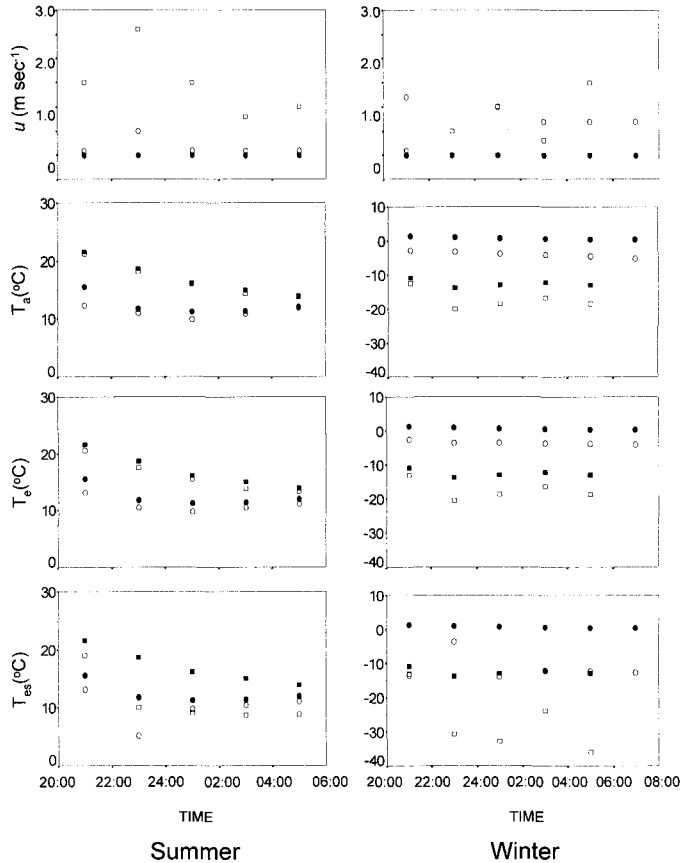


FIGURE 1. Relation of wind speed ( $u$ ), air temperature ( $T_a$ ), operative temperature ( $T_e$ ), and standard operative temperature ( $T_{es}$ ) to time of day for summer and winter birds. Shown are open sites for Mountain Chickadees (open circles) and Juniper Titmice (open squares) and cavity roosts for Mountain Chickadees (solid circles) and Juniper Titmice (solid squares).

Juniper Titmouse inside each of the nest boxes. I then placed a 15-mm wire mesh cover over the nest box opening so that the birds would not escape. I placed the birds inside the nest box shortly before sunset and allowed them to calm down before recording any microclimate data. For each of the four nights tested, there was one bird inside of each of the four nest boxes. I placed chickadees and titmice inside nest boxes at their respective study sites and tested a total of four chickadees and four titmice in each season. I measured  $T_a$  in the nest boxes using 36-gauge copper constantan thermocouple placed approximately 5-cm above each bird's head. Wind speed inside the cavities was measured on separate nights in the absence of a bird and was always below the anemometer's lowest detectable wind speed ( $< 0.05\ m\ sec^{-1}$ ) (unpubl. data). Thus, I assumed no wind inside the roost cavities.

Operative temperature thermometers ( $T_e$ ) could not be placed inside the cavity occupied by a bird. Instead  $T_e$  in the cavity was assumed to equal  $T_a$  in the cavity because it is an isothermal enclosure with no short wave radiation or forced convection (Bakken 1980).

$T_e$  helps define the sensible heat flow between a bird and its environment but it cannot establish equivalence between two environments that differ in factors that affect overall thermal conductance, notably wind (see Bakken 1992). Therefore, I calculated standard operative temperature ( $T_{es}$ ) using Bakken's (1990) (Equation 6) generalized passerine  $T_{es}$  scale:

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

$T_{es}$  was computed for both the open and cavity environment and then used to extrapolate laboratory metabolism data to the field. Nocturnal metabolism and body temperature were measured during  $T_a$  from  $-10$  to  $30^{\circ}C$  in chickadees and titmice in an earlier investigation (Cooper 1997). Microclimate data were collected from 21:00 to 05:00 in summer and from 21:00 to 07:00 in winter.

#### DATA ANALYSES

Data are presented as means  $\pm$  SE. Data for  $T_a$ ,  $T_e$ ,  $u$ ,  $T_{es}$ , and predicted metabolism were averaged for the two open sites and for the four cavities. The average

microclimate values for each 15-min interval for a given 2-hr period with the lowest temperature or highest wind speed for the entire nocturnal period were compared using Student *t*-tests because variances were equal (*F*-test for equality of variance).

## RESULTS

The extent to which the sites occupied by birds reduce their energy exchange with the environment is revealed by comparing measurements taken at open sites vs. cavity roosts (Fig. 1). For summer chickadees, the greatest difference in wind speed between the open sites and the cavity roosts occurred from 22:00 to 00:00 (Fig. 1). During this period, wind speed averaged 0.5 m sec<sup>-1</sup>. This wind speed resulted in a  $T_{es}$  of 5.1°C in the open sites compared to 11.6°C in the cavity roosts. Owing to these different convective regimes, energy expenditure over the 2-hr period for birds roosting in cavities would be reduced 34% relative to the open sites. For summer titmice, wind speed averaged 2.6 m sec<sup>-1</sup> from 22:00 to 00:00 (Fig. 1), resulting in a 38% reduction in energy expenditure for birds roosting in cavities. In summer birds, neither  $T_a$  or  $T_c$  varied significantly between open sites and cavities (*t*-tests; all  $P \geq 0.19$ ) (Table 1). Wind speed,  $T_{es}$ , and predicted energy expenditure were significantly lower in cavities than in open sites for summer titmice (*t*-tests; all  $P \leq 0.04$ ) but not for summer chickadees (*t*-tests; all  $P \geq 0.14$ ) (Table 1).

In winter,  $T_a$  within the cavity ranged from 4.3–5.6°C higher than open sites for chickadees and from 1.7–6.3°C higher for titmice. Wind speed at the open sites was higher throughout the evening for winter chickadees and titmice. The combined effect of lower  $T_c$  and greater wind speeds in the open resulted in an increased  $T_{es}$  in the cavities ranging from 4.5–14.8°C for chickadees and from 3.2–23.0°C for titmice (Fig. 1). Cavities had significantly higher  $T_a$ ,  $T_{es}$ , and  $T_{es}$  compared to open sites for chickadees and titmice (*t*-tests; all  $P \leq 0.01$ ). Wind speed was significantly higher at open sites compared to inside cavities for chickadees ( $t_{14} = 4.31$ ,  $P < 0.01$ ) and for titmice ( $t_{14} = 2.48$ ,  $P < 0.04$ ). Predicted energy expenditure in cavities was 25.1% lower for titmice and 37.6% lower for chickadees compared to open sites (Table 1).

## DISCUSSION

In summer,  $T_a$  and  $T_c$  were slightly, but not significantly, higher in cavities than in open sites. In order to separate radiative heat gain in the cavity compared to the open, vs. metabolic heating of the air within the cavity, I used Equation 1 from Bakken (1992):

$$T_c = T_a + \frac{\dot{q}}{T_R} \text{ (where } T_R \text{ is radiation conductance per } ^\circ\text{C)}$$

In summer,  $T_c$  in the open was 0.3–0.6°C lower than  $T_a$  in the open. In summer,  $T_a$  within the cavity was 0.3–1.2°C higher than the open sites. These data indicate that both radiative heat loss and metabolic heating by the bird of the air inside the cavity were of minor importance. Decreased wind speed inside the cavity accounted for the most significant thermal and energetic benefit for summer birds. Reduction in wind speed resulted in  $T_{es}$  being 2.5–4.9°C higher inside cavities compared to the open which resulted in a

TABLE 1. Average overnight microclimate variables and predicted energy expenditure (means  $\pm$  SE) at open sites compared to cavity roosts for Mountain Chickadees and Juniper Titmice for summer and winter roost periods.

Variable	31 Jul–1 Aug Mountain Chickadees		2 Aug–3 Aug Juniper Titmice		6 Feb–7 Feb Mountain Chickadees		27 Feb–28 Feb Juniper Titmice	
	Open sites	Cavity roosts	Open sites	Cavity roosts	Open sites	Cavity roosts	Open sites	Cavity roosts
Air temperature (°C)	11.3 $\pm$ 0.4	12.5 $\pm$ 0.8	16.8 $\pm$ 1.3	17.1 $\pm$ 1.4	-3.9 $\pm$ 0.4	0.9 $\pm$ 0.1*	-17.1 $\pm$ 1.3	-12.5 $\pm$ 0.5*
Operative temperature (°C)	11.0 $\pm$ 0.6	12.5 $\pm$ 0.8	16.2 $\pm$ 1.3	17.1 $\pm$ 1.4	-3.4 $\pm$ 0.2	0.9 $\pm$ 0.1*	-17.5 $\pm$ 1.2	-12.5 $\pm$ 0.5*
Wind speed <sup>a</sup> (m sec <sup>-1</sup> )	0.1 $\pm$ 0.1	0	1.5 $\pm$ 0.3	0*	0.7 $\pm$ 0.2	0*	0.7 $\pm$ 0.3	0*
Standard operative temperature <sup>b</sup> (°C)	10.0 $\pm$ 1.3	12.5 $\pm$ 0.8	11.2 $\pm$ 2.0	17.1 $\pm$ 1.4*	-11.2 $\pm$ 1.6	0.9 $\pm$ 0.1*	-27.2 $\pm$ 4.0	-12.5 $\pm$ 0.5*
Estimated energy expenditure <sup>c</sup> (kJ)	10.1 $\pm$ 1.3	7.7 $\pm$ 0.8	12.2 $\pm$ 1.1	8.8 $\pm$ 0.8*	37.2 $\pm$ 1.8	23.2 $\pm$ 0.2*	52.9 $\pm$ 3.6	39.6 $\pm$ 0.4*

<sup>a</sup> Wind speed in cavity assumed to be 0.

<sup>b</sup> Computed using Equation 1 of Bakken (1992).

<sup>c</sup> Estimate represents a 9-hr roost period in summer and a 14-hr roost period in winter. \* Indicates significant differences in intraspecific comparisons between the two sites ( $P < 0.05$ ).

23.8% reduction in nocturnal energy expenditure for chickadees and 27.9% reduction for titmice.

Air temperatures inside winter cavities were 4.6–4.8°C higher than open sites. This increase in  $T_a$  indicates that metabolic heating by the birds of air inside the cavity provides significant thermal benefits for winter-acclimatized individuals. The increased  $T_a$  inside cavities may also be due to thermal inertia of the cavities. For Acorn Woodpecker (*Melanerpes formicivorus*) cavities, with one bird inside, thermal inertia accounted for 4.3 of a total of 5.5°C increase in  $T_a$  compared to open sites (du Plessis et al. 1994). However, the chickadee and titmouse artificial cavities were held at outside  $T_a$  and kept shaded until microclimate measurements began. Thus, it is unlikely that the cavities would have been warmer than the surrounding  $T_a$  and that thermal inertia is responsible for the increased  $T_a$  inside the cavities. However, for natural cavities, it is possible that thermal inertia of cavities would cause an even greater increase in  $T_a$  compared to roosting in the open. Reduction of wind speed inside the cavities in winter resulted in an increased  $T_{es}$  of 12.1°C for chickadees and 14.7°C for titmice compared to open sites. This significant increase in  $T_{es}$  results in a nocturnal energy savings of 25.1% for winter titmice and 37.6% for winter chickadees.

Reduction of nocturnal energy metabolism due to cavity roosting is important for chickadees and titmice because nocturnal energy savings translate to increased fasting endurance. I determined the increase in fasting endurance due to cavity roosting by subtracting predicted nocturnal energy expenditure for birds roosting in cavities from the predicted nocturnal energy expenditure for birds roosting in the open for the four nights that microclimate data were measured. I took these energy metabolism values and divided them by the resting metabolic rate of chickadees and titmice at the mean daily temperature for each season. This results in the amount of time that a bird can fast while maintaining resting metabolism. For summer birds, fasting endurance increased 2.2 hr for chickadees and 3.0 hr for titmice roosting in cavities compared to open sites. For winter birds, fasting endurance increased 7.3 hr for chickadees and 5.7 hr for titmice. For summer birds, additional fasting endurance may be important in allowing adults to feed nestlings especially upon leaving the roost. For winter birds, increased fasting endurance may be especially important during inclement weather that might reduce foraging ability.

My analysis demonstrates the importance of cavity roosts on reduction in convective heat loss in Mountain Chickadees and Juniper Titmice. In addition, in winter, it appears that metabolic heating of the air within the cavity is an important thermal benefit for these two species. Clearly, use of cavity roosts by chickadees and titmice offer significant nocturnal energy savings, which translates into increased fasting

endurance important throughout the annual cycle of these birds.

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