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Potential energy expenditure by litter-roosting bats associated with temperature under leaf litter during winter



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ABSTRACT

In temperate portions of North America, some bats that remain active during winter undergo short periods of hibernation below leaf litter on the forest floor during episodes of below-freezing weather. These winter roosts may provide above-freezing conditions, but the thermal conditions under leaf litter are unclear. Further, little is known of the relationship between temperatures under litter and potential energy expenditure by bats. Therefore, I characterized thermal conditions below leaf litter, compared temperatures encountered under different litter depths, and evaluated the quality of these sites as hibernacula based on potential energy use by eastern red bats (*Lasiurus borealis*) during winter in forests of the Ouachita Mountains, Arkansas, USA. Over an averaged 24-h period, there was no significant difference in temperature among different depths of leaf litter, but temperatures under litter remained significantly warmer than air temperatures, especially during nighttime and under snow cover. Temperatures below leaf litter were significantly warmer on south-facing slopes than north-facing slopes, but predicted metabolic rates did not differ among aspects. Predicted metabolic rates of eastern red bats were lowest under the deepest leaf litter measured (8 cm) and highest under ambient air conditions. Depending on depth of leaf litter cover, predicted energy savings based on O₂ consumption from roosting under litter were 1.9 to 3.1 times greater than remaining in ambient air during periods of freezing weather and around 5.6 times greater when roosting under leaf litter with snow cover. A model for predicted total energy consumption (estimated as the total oxygen consumption during a 24-h period) by eastern red bats indicated that when roosting below leaf litter, energy consumption would be reduced with greater ground temperatures, greater leaf litter moisture, and when located on south-facing slopes. Predicted metabolic rates and total energy consumption may provide more insight on the quality of roost sites for wintering bats than temperature of roost sites alone.

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1. Introduction

In temperate North America, some bat species, including eastern red bats (*Lasiurus borealis*) and silver-haired bats (*Lasionycter noctivagans*), migrate from northern portions of their range to more southerly latitudes during winter to escape harsh winter conditions (Davis, 1970). At these more southerly latitudes, they typically remain active during winter and roost in forests (e.g., Mormann and Robbins, 2007; Perry et al. 2010). During winter, foliage-roosting species, including eastern red bats and Seminole bats (*L. seminolus*), roost in tree foliage during relatively warm winter periods (> 10 °C), but retreat to the forest floor where they hibernate for short periods under leaf litter during colder periods (Mormann and Robbins, 2007; Hein et al., 2008). For these species, mortality during winter may be high (Cryan and Veilleux, 2007), and roost sites selected by these

bats during winter may be especially important to their survival. For example, 21% of 33 eastern red bats radio tracked during winter succumbed to freezing or predators (Flinn, 2009).

Eastern red bats are found throughout the southeastern U.S. during winter, from New Jersey to central Texas (Cryan, 2003). Western red bats (*Lasiurus blossevillii*) have also been found to use leaf litter roosts during winter in California (Johnston and Whitford, 2009). Furthermore, other North American bat species that remain active in forests during winter at these latitudes but do not roost in foliage, including silver-haired bats and evening bats (*Nycticeius humeralis*), may occasionally hibernate in below-ground roosts such as small mammal burrows or rock crevices during periods of below-freezing weather (Boyles et al., 2005; Perry et al., 2010). Bats roosting under leaf litter or just below the soil surface during winter typically experience warmer and more stable temperatures than remaining in trees during colder periods, primarily during nighttime (Boyles et al., 2005; Mormann, 2005; Flinn, 2009), and deeper leaf litter may result in more stable temperatures (Mormann, 2005). Thus, hibernating for short periods below leaf litter or just below the

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soil surface during periods of freezing weather appears to be a widespread phenomenon in many bat species that remain active during winter in temperate regions of North America.

To extend fat reserves and reduce energy expenditure, bats undergo periods of torpor. When food resources are limited or environmental conditions are unfavorable, bats undergo extended periods of torpor lasting ≥ 2 days, which is considered hibernation (e.g., [Speakman and Thomas, 2003](#)). During torpor, metabolic rates are reduced (torpid metabolic rates; TMR), along with heart rate, oxygen consumption, and body temperature ([Hock, 1951](#)). During torpor, body temperatures may be close to ambient temperatures and TMR is thus limited by the surrounding ambient temperatures (e.g., [Hock, 1951](#)). Hibernation is associated with deep torpor, where body temperatures may fall to 2 °C and may involve additional metabolic suppression ([Speakman and Thomas, 2003](#)). During hibernation, low (e.g., 5 °C), but above freezing temperatures allow the deepest torpor and greatest energy savings, but bat species may differ in the ambient temperature at which they reach minimum TMR (e.g., [Speakman and Thomas 2003](#); [Dunbar and Brigham, 2010](#)).

Unlike many temperate, cave-hibernating bat species that typically arouse at ambient temperatures of 10 to 15 °C during hibernation, eastern red bats typically become euthermic at temperatures above 20 °C ([Davis and Reite, 1967](#)), but these higher temperatures may allow bats to forage on available insects during above-freezing nights of winter ([Davis, 1970](#); [Dunbar and Tomasi, 2006](#); [Dunbar and Brigham, 2010](#)). During hibernation, captive eastern red bats from Missouri may maximize energy savings (lowest TMR) at ambient temperatures of approximately 5–10 °C, but may increase their metabolism when temperatures fall below this level, and increase their metabolism substantially when ambient temperatures fall below freezing ([Dunbar and Tomasi, 2006](#)). During torpor, eastern red bats can withstand greater fluctuations in temperature without arousing than many other temperate bats ([Davis and Reite, 1967](#)) and are relatively efficient metabolic regulators at subfreezing temperatures, having fur-covered uropatagiums that they wrap around their bodies to retain metabolic heat when temperatures fall below freezing ([Davis, 1970](#)). All of these adaptations allow eastern red bats to hibernate in more harsh and fluctuating climatic conditions than many other temperate bat species.

Historically, most studies comparing the quality of hibernation habitat for bats have focused on abiotic factors of their roosts such as temperature and humidity (e.g., [Perry, 2013](#)) or compared abiotic factors between sites where bats were found with sites not occupied (e.g., [Sherwin et al., 2003](#)). These studies suggested that sites occupied by bats provided optimal conditions but rarely compared the energetic costs among sites over time. Although factors such as predation risk and disturbance frequency likely affect hibernacula selection by bats, variability in hibernacula microclimate and amount of time hibernacula microclimates fall above or below important metabolic thresholds likely influences overall suitability of these sites as well. Thus, comparing the potential energy expenditure by bats among sites may provide additional insight when comparing different hibernacula locations. Furthermore, the association between thermal conditions that torpid bats encounter under in leaf litter during winter and the potential energy savings of these roosts remain unstudied. The goals of this study were to: (1) characterize the thermal conditions encountered below leaf litter during winter; (2) compare temperature profiles among different litter depths, below the soil surface (ground), and ambient air conditions; (3) evaluate the effects of slope aspect on thermal conditions beneath leaf litter; and (4) evaluate and compare the quality of these sites based on predicted metabolic rates and potential energy use of eastern red bats.

2. Materials and methods

2.1. Study area

The study was conducted in, and adjacent to, the Alum Creek Experimental Forest of the Ouachita National Forest in the Ouachita Mountains of west-central Arkansas, USA. The Ouachita Mountains consist of east–west oriented mountains and valleys that extend from central Arkansas into east-central Oklahoma. Elevation in the study area is approximately 207–780 m. The study area is approximately 7000 ha, and consists of mixed shortleaf pine (*Pinus echinata*) and hardwood forest. The hardwood component of these forests is diverse (>32 species) but was primarily *Quercus* sp. (oaks), *Carya* sp. (hickories), and Red Maple L. (*Acer rubrum*).

Climate of the region is humid subtropical. Based on data from the Alum Fork weather station (approximately 5 km from the study area), mean (max/min) winter temperatures (for the years 1971 to 2000) was 15.4/3.5 °C for November, 10.3/–0.9 °C for December, 8.8/–2.8 °C for January, 11.9/–0.9 °C for February, and 16.6/3.7 °C for March ([NCDC, 2004](#)). Yearly mean precipitation was about 140 cm, and mean annual snowfall was about 13 cm ([NCDC, 2004](#)).

2.2. Temperature measurements

I identified 26 sites that represented typical leaf-litter roost locations for eastern red bats during winter; sites were located on upper slopes near ridge tops in areas that had relatively abundant hardwood leaf litter ([Mormann and Robbins, 2007](#); [Flinn, 2009](#)). Sites were selected from maps of topography and forest conditions based on the following criteria: (1) upper slope or ridge top areas; (2) north-facing and south-facing slopes in relatively close proximity; and (3) mature timber with a hardwood component. Areas that had been subjected to prescribed burning <2 years prior were avoided. At each site, one plot was randomly established on a north-facing slope and one on a south-facing slope ($n=52$ total plots) to sample thermal properties under leaf litter.

At each plot, thermocouples (CASS-18G-12-NHX, Omega Engineering, Stamford, CT) attached to Hobo data loggers (U12-014, Onset Computer, Corp., Cape Cod, MA) were placed beneath deciduous leaf litter to determine temperature (°C) profiles under three different litter depths. Temperature was recorded every 30 min. At each plot, a thermocouple was placed: (1) below 2 cm of leaf litter (T_2); (2) below 5 cm of leaf litter (T_5); (3) below 8 cm of leaf litter (T_8); (4) 2 cm below the soil surface (ground temperature; T_g); and (4) elevated 1 m above the ground to record air temperature (T_a). When temperature was measured below leaf litter, duff was not removed from plots and thermocouples were placed above the duff layer.

Plots were sampled only when forecasted low temperatures were expected to be close to or below freezing ($n=15$ days). During each sample day, one or two sites (2 or 4 plots) were sampled over a 24-h period (1800–1800 CST the next day). Sampling took place during two winters between 14 November and 3 March (2011–2013). Three plots (all north-facing slopes) had malfunctioning units. Thus, these plots and their corresponding plots on south-facing slopes were removed from analysis so that each site had a corresponding north- and south-facing slope where temperature data was recorded over the same 24-h period ($n=46$ plots total).

To determine environmental factors aside from leaf-litter depth that may influence potential energy use by eastern red bats under leaf litter, a set of parameters predicted to affect temperature in plots was collected. At each plot, basal area of pines was recorded using a 10-factor English prism (converted to metric; m^2/ha) and canopy cover (%) was estimated using a spherical densiometer. Moisture content of leaf litter (%) was estimated by removing litter

to the duff layer in a $0.3 \times 0.3 \text{ m}^2$ area, drying at 60°C to constant mass, and comparing with wet mass. Average leaf litter depth (cm) was also measured using five random samples at each plot.

Approximately 25 cm of snow fell during one period of the study and remained for approximately 12 days. Estimated snow depth during the 24-h period when temperature measures were taken was 8–13 cm. Temperature measures were taken in four plots (2 north- and 2 south-facing slopes) under the snow over a single 24-h period. These data were not included with other temperature measures, and analysis on these data was not conducted because of small sample size ($n=4$ plots). However, these data were presented as an illustration of the effects of snow cover on thermal conditions below leaf litter.

2.3. Analyses

Temperature profiles taken every 30 min were averaged for nighttime (1700–0800), daytime (0800–1700), and for the entire 24-h period for analysis. Temperature readings recorded in each thermocouple position (T_a , T_2 , T_5 , T_8 , and T_g) were compared over time using a repeated-measures ANOVA with aspect (north- or south-facing slope) as an additional fixed effect. Interactions of thermocouple position \times aspect were also examined. To determine the best covariance matrix to use, values of Akaike's information criterion (AIC) were compared among five models that used different covariance matrices (variance components, compound symmetry, Toeplitz, first-order autoregressive, and Huynh-Feldt; Littell et al., 2006; SAS Institute Inc., 2009). A Toeplitz covariance matrix had the best fit for these data. Kenwood–Roger adjustments were used to generalize degrees of freedom (Littell et al., 2006). When ANOVA indicated a significant difference among treatments, a Tukey's adjustment was used to separate least-squared means (SAS Institute Inc., 2009). All tests were evaluated at $\alpha=0.05$.

Estimates of metabolic rate ($\text{O}_2 \text{ ml/h}$) based on ambient temperatures for eastern red bats were modeled from Dunbar and Tomasi (2006); they estimated mean metabolic rate for captive eastern red bats at five temperatures (-5 , 1 , 5 , 10 , and 15°C) during hibernation (Fig. 1). Metabolic rates associated with ambient temperatures from 1 to 15°C were torpid rates, but bats became euthermic at -5°C (Dunbar and Tomasi, 2006). Above 20°C , red bats likely become euthermic as well (Davis and Reite, 1967). Thus, metabolic rates at ambient temperatures $\leq -5^\circ\text{C}$ and $\geq 20^\circ\text{C}$ were considered euthermic metabolic rates. Although euthermic metabolic rates for red bats at ambient temperatures $> 15^\circ\text{C}$ were not available, I assumed euthermicity at 20°C would result in a substantial increase in metabolic rate, similar to results for hoary bats (*Lasiurus cinereus*) (Cryan and Wolf, 2003). Nevertheless, ambient temperatures recorded $> 15^\circ\text{C}$

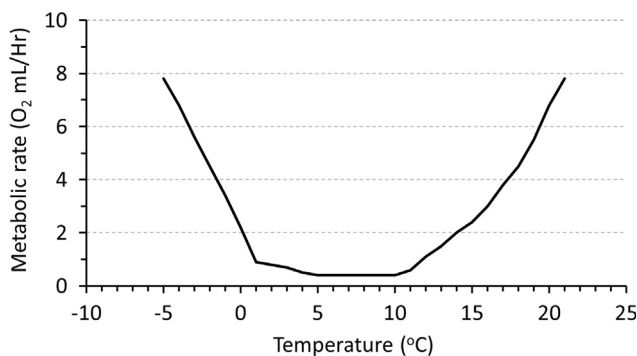


Fig. 1. Model of the relationship between metabolic rates and ambient temperatures for eastern red bats during winter used to predict metabolic rates and energy consumption in different hibernacula locations. Mean metabolic rates for -5 , 1 , 5 , 10 , and 15°C were from Dunbar and Tomasi (2006). At temperatures ≤ -5 and $\geq 20^\circ\text{C}$, bats were assumed to be euthermic.

accounted for only 1.9% of total temperature measurements. I used similar metabolic rate values for all ambient temperatures above 20°C and similar values for all temperatures below -5°C . For each 30-min temperature recording, I calculated predicted metabolic rates for that temperature and calculated mean values for night, day, and an entire 24-h period.

To compare predicted metabolic rates among different depths of leaf litter and ambient air conditions, a repeated-measures analysis similar to above was used. For the metabolic rate data, I used the Toeplitz covariance matrix, which had the lowest AIC values among the five models compared (Littell et al., 2006). Metabolic data were rank transformed prior to analyses because of skewedness that could not be corrected via transformation (Conover and Iman, 1981).

To determine environmental factors that likely affected energy expenditure aside from leaf litter depth, I compared 15 a priori, multiple-regression models. The dependent variable was predicted total metabolic oxygen consumption by eastern red bats over a 24-h period under 5 cm of leaves. Total O_2 consumption was used as a surrogate for total energy use. I used 5 cm of leaves because this was close to the average depth of leaf litter from plots ($4.5 \pm 0.2 \text{ cm}$). Independent variables that were predicted to affect roost temperatures included in the models were mean ground temperature (T_g), Aspect (north- or south-facing slopes), litter moisture (LitMoist; %), and canopy cover (Cover; %) at each plot. Pine basal area was highly correlated with Cover ($r=0.84$) and was removed. I determined the most parsimonious set of models among candidate models based on the value of AIC modified for small samples (AIC_c ; Burnham and Anderson, 2002). No models were within 2 units of AIC_{\min} ; thus, model averaging of the best set was not necessary (Burnham and Anderson, 2002).

3. Results

3.1. Temperatures below leaf litter

Average high air temperature (T_a) of sampling days was 11.4°C and average low was -3.3°C (range -9.4 to 20.3). With daytime and nighttime combined, mean temperatures differed significantly among the thermocouple positions ($F_{4, 219}=16.27$, $P<0.001$); there was no significant difference in temperature among leaf litter depths (T_2 , T_5 , and T_8), but all three depths were significantly warmer than T_a and significantly cooler than T_g (Fig. 2). Effect of aspect was also significant for the 24-h period ($F_{1, 219}=13.50$, $P<0.001$), with south-slope locations significantly warmer than north-slope locations. There was not a thermocouple position \times aspect interaction ($F_{4, 219}=0.61$, $P=0.658$).

During daytime (0800–1700), mean temperatures did not differ among any of the thermocouple positions ($F_{4, 218}=1.40$, $P=0.235$), but south slope locations had significantly warmer temperatures than north slopes ($F_{1, 218}=16.3$, $P<0.001$). There was not a significant thermocouple position \times aspect interaction ($F_{4, 218}=0.32$, $P=0.864$). During nighttime (1700–0800), temperatures differed among the thermocouple positions ($F_{4, 214}=28.24$, $P<0.001$), and south-slope plots had significantly warmer temperatures than north-slope plots ($F_{1, 214}=7.17$, $P=0.008$); there was not a significant thermocouple location \times aspect interaction ($F_{4, 214}=0.53$, $P<0.714$). At night, T_8 was significantly warmer than T_2 , T_5 and T_8 were significantly warmer than T_a , and T_g was significantly warmer than T_a and all depths of leaf litter.

3.2. Temperatures below snow cover

No temperature difference was discernible among the three leaf-litter depths when covered by 8–13 cm of snow, although

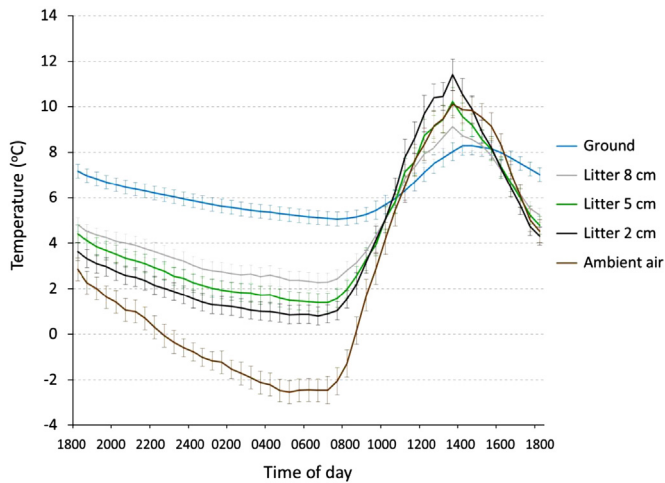


Fig. 2. Mean temperature ($n=46$ plots; 23 on north and 23 on south aspects) and standard error bars taken every 30 min over a 24-h period for ground temperature 2 cm below the soil surface (T_g), below 3 depths of leaf litter (8 cm [T_8], 5 cm [T_5], and 2 cm [T_2]), and ambient air (T_a) taken over 15 below-freezing nights during winter (late November–early March) in the Ouachita Mountains of Arkansas, 2011–2013.

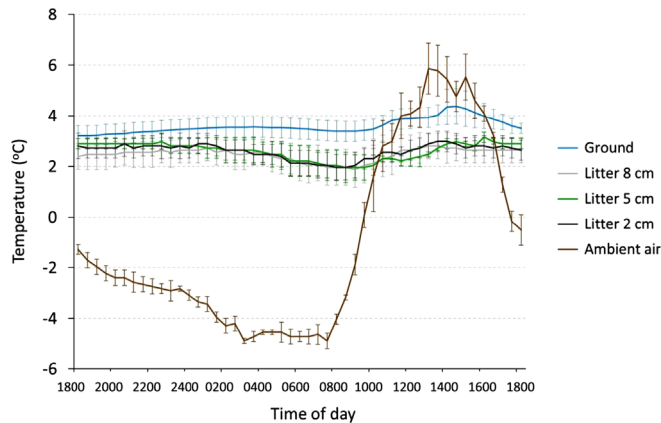


Fig. 3. Mean temperatures ($n=4$ plots; two on north and two on south aspects) and standard error bars taken every 30 min over a 24-h period for ambient air (T_a), ground temperature 2 cm below the soil surface (T_g), and below three depths of leaf litter (8 cm [T_8], 5 cm [T_5], and 2 cm [T_2]) with 8–13 cm of snow cover during winter in the Ouachita Mountains of Arkansas, 2011–2013.

compression by snow may have reduced the thermal insulation provided by different litter depths (Fig. 3). Nevertheless, temperatures under all litter depths and T_g remained well above freezing during this time even though mean T_a fell to -5°C during the night. Under snow, variability in temperature during a 24-h period was greatly reduced compared to conditions beneath leaf litter without snow (Fig. 2). Under snow, temperatures below leaf litter remained approximately 7°C warmer than the T_a during the coldest period of the night, whereas temperatures below litter were approximately 4°C warmer than T_a without snow present.

3.3. Predicted metabolic rates of eastern red bats

Daily mean predicted metabolic rates derived from temperature differed significantly among all thermocouple positions ($F_{4, 220}=102.49$, $P<0.001$), with T_g and T_8 having the lowest average metabolic rates and T_a having the greatest (Fig. 4). Plots located on north- and south-facing slopes did not differ during a 24-h period ($F_{1, 220}=0.00$, $P<0.945$), nor was there a significant interaction between slope aspect and thermocouple position ($F_{4, 220}=0.98$, $P<0.418$).

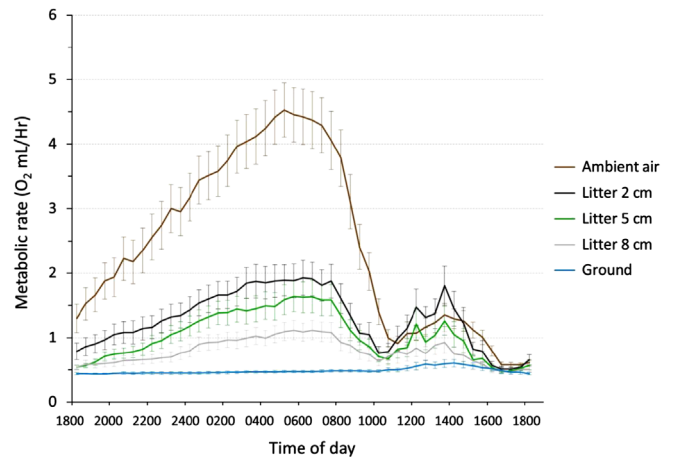


Fig. 4. Mean metabolic rates and standard error bars for eastern red bats predicted over a 24-h period derived from temperatures (using values presented by Dunbar and Tomasi, 2006) recorded for ambient air (T_a), below 3 depths of leaf litter (2 cm [T_2], 5 cm [T_5], and 8 cm [T_8]), and 2 cm below the soil surface (T_g), recorded over 15 below-freezing nights in the Ouachita Mountains of Arkansas, 2011–2013.

When analyzed by day and night separately, mean metabolic rates differed among thermocouple positions both during nighttime ($F_{4, 217}=59.81$, $P<0.001$) and daytime ($F_{4, 195}=25.38$, $P<0.001$). During nighttime, predicted metabolic rates associated with T_a were greatest, followed by T_2 , T_5 , and T_8 ; T_2 and T_5 did not differ significantly nor did T_5 and T_8 . During the afternoon period of 1200–1600, predicted T_2 metabolic rate was generally greater than other locations due to solar heating. However, during the overall daytime period (0800–1700), predicted metabolic rate associated with T_a was greatest, followed by T_2 , T_5 , and T_8 ; T_2 and T_5 did not differ, T_5 and T_8 did not differ, and T_2 did not differ significantly from T_a . Metabolic rates derived from T_g were significantly lower than other locations during both daytime and nighttime. For T_a , predicted metabolic rate went up during the night due to below-freezing temperatures and went up again during the day due to warm temperatures. This pattern was also seen under all depths of leaf litter, but less so in T_8 . The periods of lowest predicted metabolic rate based on temperature in T_a were approximately 1100 and 1700, with below-litter values following a similar trend but delayed by approximately 1 h.

During nighttime, predicted metabolic rate was greater on north-facing slopes than on south slopes ($F_{1, 217}=3.96$, $P=0.048$), and there was not a significant thermocouple position \times aspect interaction ($F_{4, 217}=1.39$, $P=0.239$). During daytime, predicted metabolic rate was generally greater on south slopes than north slopes, but this trend was not significant ($F_{1, 195}=3.38$, $P=0.067$); there was not a significant aspect \times thermocouple position interaction ($F_{4, 195}=0.36$, $P=0.839$). For an entire 24-h period, predicted TMR did not differ between north- and south-facing slopes.

Predicted mean metabolic rate over a 24-h period was 3 times greater in T_a than T_8 (Table 1). Based on total O_2 consumption predicted over a 24-h period with below-freezing nights, compared to ambient air conditions, roosting at T_2 was 1.9 times more efficient, roosting at T_5 was 2.4 times more efficient, roosting at T_8 was 3.1 times more efficient, and roosting at T_g was 5.1 times more efficient (Table 1). Roosting under leaf litter during a snow event would have resulted in 5.6–5.7 times less energy use than roosting at T_a and roosting at T_g during snow events would have resulted in 7.5 times less energy use than roosting at T_a .

3.4. Factors affecting potential energy expenditure

One regression model ($R^2=0.41$) relating total potential consumption of oxygen (ml) to environmental conditions was deemed

Table 1

Predicted mean metabolic rate, total O₂ use, and total O₂ use with 8–13 cm of snow cover for a 24-h period, based on temperature measures taken every 30 min over a 24-h period for ambient air, below 3 depths (cm) of leaf litter (T_2 , T_5 , and T_8), and ground temperature 2 cm below the soil surface (T_g) recorded over 15 below-freezing nights during winter (late November–early March) in Arkansas.

Location	Predicted mean metabolic rate (ml O ₂ /h)	Predicted total O ₂ use (ml)	Predicted total O ₂ use with snow cover (ml)
Air (T_a)	2.4	59.2	92.2
Under 2 cm of leaf litter (T_2)	1.3	31.2	16.2
Under 5 cm of leaf litter (T_5)	1.0	25.1	16.5
Under 8 cm of leaf litter (T_8)	0.8	19.1	16.3
Ground (T_g)	0.5	11.6	12.3

Table 2

Akaike's information criterion for small samples (AIC_c), difference (Δ AIC_c) between AIC_c and the best-approximating model (AIC_{min}), AIC_c weights (ω_i), and R^2 for linear regression models within 2 units of AIC_{min} for models comparing plot-level variables with predicted total oxygen consumption (ml) by eastern red bats over a 24-h period under 5 cm of leaves in the Ouachita Mountains of Arkansas, 2011–2013.

Model	AIC _c	Δ AIC _c	ω	R^2
T_g + LitMoist + Aspect	239.774	0.00	1.00	0.40
T_g + LitMoist + Aspect + Cover	242.023	2.24		
T_g + LitMoist	242.118	2.34		
T_g + LitMoist + Cover	244.032	4.26		
T_g + Aspect	244.899	5.13		
T_g + Aspect + Cover	247.174	7.40		
T_g	248.469	8.69		
T_g + Cover	250.458	10.68		
Aspect	258.010	18.24		
LitMoist	258.233	18.46		
Aspect + Cover	259.160	19.39		
Cover	259.685	19.91		
Aspect + LitMoist	260.098	20.32		
Cover + LitMoist	260.392	20.62		
Cover + LitMoist + Aspect	261.871	22.10		

T_g =ground temperature at 2 cm depth.

LitMoist=percent moisture in leaf litter.

Aspect=1 for north slopes and 0 for south slopes.

Cover=percent forest canopy cover.

to be the best model based on values of AIC_c (Table 2). No other models were within 2 units of AIC_{min}. This model included the estimated ground temperature (T_g), the percent of moisture in the leaf litter (%), and the aspect (north- or south-facing slopes); mean canopy cover was not included in this model. This model was:

Total O₂ use (ml) over a 24-h period under 5 cm of leaves during winter with below-freezing nights = $85.41 - 5.02(T_g) - 0.54(\text{LitMoist}) - 8.43(\text{Aspect})$, where aspect = 1 for north-facing slopes and aspect = 0 for south-facing slopes. Based on this model, total potential energy expenditure decreased with greater T_g , greater leaf-litter moisture, and when on south slopes. Standardized parameter estimates (and 95% confidence intervals) were -0.26 (-0.52 to -0.09) for aspect, -0.36 (-0.63 to -0.09) for litter moisture, and -0.68 (-0.96 to -0.41) for T_g , suggesting ground temperature had the greatest effect on the model.

4. Discussion

Similar to cave climates used by other bat species, leaf litter provides an important thermal refuge for bats during the winter,

which buffers them from extreme fluctuations in temperature and provides cold, but above-freezing temperatures most of the time. Eastern red bats should encounter substantial energy savings by roosting below even a shallow layer of leaves when nighttime air temperatures fall below freezing. Depending on depth of leaf litter cover, predicted energy savings over a 24-h period based on O₂ consumption from roosting under litter was 1.9 to 3.1 times greater than remaining in ambient air during days with below-freezing nighttime temperatures. This savings was especially pronounced when snow cover was present, with around 5.6 times less energy use predicted under leaf litter and snow compared to roosting in ambient air conditions. During nighttime, deeper leaf litter provided greater metabolic savings, but mean predicted metabolic rate over a 24-h period beneath as little as 2 cm of litter (equivalent to a single layer of leaves) was significantly less than that in ambient air.

Daily temperatures (both air and below leaf litter) followed a sine wave curve, with temperatures peaking during daylight hours and reaching lows just before sunrise, similar to results found in other studies of bats under leaf litter (e.g., Mormann, 2005; Flinn, 2009) and similar to studies of soil temperature (Jury et al., 1991). Like measurements taken in soils, a time lag also occurred, with temperatures continuing to cool after sunrise and shallower depths below litter warming more quickly (Jury et al., 1991).

Ground temperatures conducted heat into the leaf litter, and the temperature at greater depths below the soil surface is expected to be near the mean annual temperature of a region (e.g., Witkamp, 1969; Perry, 2013). Long-term cold spells would cause frost deeper into the soil, reducing the benefits created by thermal conduction from the ground. However, long-term cold spells where air temperatures remained below freezing for multiple days or weeks did not occur during the study and the longest period when air temperatures remained below freezing was 2–3 days. Thus, ground temperatures likely conducted heat into the leaf litter during most of the study.

The model to isolate potential factors affecting overall energy expenditure aside from litter depth indicated that eastern red bats under 5 cm of leaf litter would use less energy with greater ground temperatures, increased litter moisture, and when plots were on south-facing slopes. Greater ground temperatures conducted more heat into the leaf litter, which maintained greater overall litter temperatures. However, ground temperatures declined throughout the winter, from around 8.9 °C in November to around 4.1 °C in February. Thus, thermal benefits of roosting under leaf litter likely declines as winter progresses. Because of the relatively high specific heat of water compared to air, moist leaf litter likely diminishes fluctuations in temperature encountered below the leaf litter compared with dry litter. Moist litter likely cools slower during the night and warms less quickly during the day than dry litter. During hibernation, bats are susceptible to dehydration due to high rates of evaporative water loss, which is mostly through the skin because of their relatively large, naked wing membranes (e.g., Hattingh, 1972; Thomas and Cloutier, 1992). Moist litter may also reduce evaporative water loss by bats in hibernation because of the high moisture environment.

Overall temperatures in plots (including nighttime, daytime, and over an entire 24-h period) were greater on south-facing slopes than north-facing slopes. At intermediate latitudes (e.g., 30–60° north), temperature of the soil is greater on southern slopes than northern slopes, and greater variation in temperature occurs between day and night on south-facing slopes than on north-facing slopes (Jury et al., 1991). Although temperatures generally decrease with increasing elevation, lower elevations in areas of rolling topography may be cooler due to cold air sinking into valleys during winter nights (Barry, 1992). In an area with topography similar to that of this study, mean air temperatures were significantly greater on upper south slopes than on lower north or lower

south slopes, and a bat roosting in leaf litter on a lower north-slope died, most likely from hypothermia (Flinn, 2009).

Whether bats choose to roost on north or south slopes across a landscape may be affected by latitude and the mean winter temperature of an area (Mormann, 2005). Eastern red bats roosting in leaf litter during winter at 36.6–37.0° latitude (average winter temperature = 4.5 °C) were mostly on south-facing slopes where temperatures were greater (Mormann and Robbins, 2007; Flinn, 2009). Eastern red bats at 34.5° latitude (average winter temperature = 6.6 °C) roosted mostly on north slopes where lower temperatures may have allowed deeper torpor (Saugey et al., 1998). Although predicted mean metabolic rate was greater on north slopes during nighttime, predicted metabolic rates did not differ between north and south slopes over a 24-h period in this study. Based on modeling, aspect affected overall energy expenditure, but less so than ground temperatures or leaf-litter moisture. Consequently, the benefits of roosting on north slopes versus south slopes may also be affected by the length of preceding cold spells and whether it is early or late winter. The latter two factors affect ground temperatures, which ultimately affect temperatures encountered and energy use under leaf litter.

Frequently burned areas have significantly shallower leaf litter than areas that are not burned (e.g., Perry et al., 2009), and eastern red bats may disproportionately use areas for roosting that are not burned compared to burned areas during winter (Flinn, 2009). However, Mormann (2005) found 77% of leaf litter roosts during one year were in areas that were burned the previous spring, whereas during the next winter, no roosts were in areas that were burned in the previous year, suggesting that site fidelity greatly affected roost locations. Prescribed burns conducted during winter could eliminate habitat for eastern red bats for the remainder of the winter, whereas burns conducted prior to leaf fall (late spring, summer, or early fall) would have less impact and provide at least a shallow layer of leaves. Furthermore, large, landscape-level burns conducted during winter may make finding suitable winter roosting habitat difficult for eastern red bats within their winter home range.

Eastern red bats may remain under leaves during periods of snow cover (Mormann et al., 2004). Similarly, Ussurain tube-nosed bats (*Muriana ussuriensis*) in Japan have been found buried in deep snow during winter where they likely remain in torpor until early spring (Hirakawa and Kosaka, 2009). Temperatures under leaf litter in my study remained substantially above freezing when covered by snow. Average ground temperature during this snow cover was 3.6 ± 0.04 °C, which conducted heat into the leaf litter. Thus, snow acted as a blanket and provided relatively constant, above-freezing temperatures under leaf litter when ground temperatures were above freezing. Snowpack provides insulative cover for mammals in northern latitudes and high elevations, and temperatures below the snowpack often remain near 0 °C even though air temperatures of –10 to –20 °C are recorded (e.g., Merritt, 1984; Sharratt et al., 1992; Happold, 1998). Melting near the bottom of snowpacks caused by warmer ground temperatures may provide subnivean spaces for terrestrial small mammal movements (Marchand, 1996). Further, high mortality of small mammals during winter at northern latitudes or high-elevation areas may be due to a lack of snowcover that insulates the forest floor against cold air temperatures (e.g., Pruitt, 1957).

During the period of snow cover, diurnal temperatures were above freezing, but nighttime temperatures fell below freezing. Thus, the daily melting and re-freezing cycle of the snow produced a sheet of ice on the snow surface, which would have been impossible for a bat to break through. Consequently, a bat would have been trapped under the snow during the 12-day period of snow cover. Mormann and Robbins (2007) found eastern red bats remained under leaf litter for an average of 12.1 days, and Flinn (2009) found eastern red bats remained in leaf-litter roosts up to

40 days, which suggests eastern red bats may remain stationary (and presumably in hibernation) for substantial periods. The level of oxygen available under this snow cover and the size of the subnivean space was unknown. However, the low O₂ consumption of bats in deep torpor may allow bats to remain under snow cover for prolonged periods under relatively low oxygen conditions provided by small subnivean spaces.

Although metabolic rate of bats was not directly measured in this study, calculating metabolic rates of free-ranging bats beneath different depths of litter under realistic field conditions was not feasible. Extrapolating metabolic rates based on the ambient conditions associated with roost locations provide insight into the energetic savings bats could potentially encounter. Eastern red bats undergo bouts of hibernation during cold periods, but may arouse and foraging during warmer periods. Therefore, results of this study pertain only to predicted metabolic rates during periods when nighttime temperatures fall below freezing and does not account for longer-term arousals that may occur during longer periods of warm winter temperatures. Although arousal frequency at different temperatures has been estimated (Dunbar and Tomasi, 2006), variability in weather throughout winter and among years, and energy expended and gained during foraging bouts makes determining total winter energy budgets problematic for eastern red bats.

Using observed temperatures to predict metabolic rates and energy use over time provides a useful tool to determine the physiological benefits or disadvantages of different roost sites. Unfortunately, metabolic rates (both torpid and euthermic) associated with a range of temperatures are currently not available for most North American bat species (Perry, 2013). Although the energy expenditure of bats can be used to evaluate roost quality, other factors such as predation risk may also play a role in roost selection. Bats may encounter increased predation risk when roosting on the ground during cold periods. Although torpid eastern red bats roosting in trees during winter are likely susceptible to avian predators, their cryptic coloration, roosting among residual leaves of similar color, and their height above the ground likely reduce predation pressures at these locations. Terrestrial predators using olfactory clues could easily locate and consume bats beneath the leaf litter; thus, they likely minimize the amount of time they roost in the leaf litter. There are likely trade-offs between energy savings during colder periods, risk of freezing, and predation.

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