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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 O_2 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 (*Lasionycteris 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