



Physiological and behavioral adaptations in bats living at high latitudes



Justin G. Boyles^{a,*,1}, Liam P. McGuire^{b,1}, Esmarie Boyles^a, Jesika P. Reimer^c, Christopher A.C. Brooks^a, Robert W. Rutherford^d, Teresa A. Rutherford^d, John O. Whitaker Jr.^e, Gary F. McCracken^f

^a Cooperative Wildlife Research Laboratory, Department of Zoology, Southern Illinois University, Carbondale, United States

^b Department of Biological Sciences, Texas Tech University, Lubbock, United States

^c Alaska Center for Conservation Science, University of Alaska Anchorage, United States

^d 61.5 Tok Cutoff, Slana, Alaska, United States

^e Department of Biology, Indiana State University, Terre Haute, United States

^f Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, United States

HIGHLIGHTS

- Little brown bats in Alaska have less time to forage than more southerly bats.
- However, they have similar daily energy expenditure.
- They have high energy intake rates compared to more southerly bats.
- It appears that a shift to consuming spiders facilitates energy balance.

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ABSTRACT

Widespread animals at the extremes of the species' distribution experience ecological constraints different than individuals in the core of the distribution. For example, small endotherms at very high latitudes face short summers with cool temperatures and a lack of true darkness. In particular, insectivorous bats at high latitudes may experience constraints because of their unique life history traits, and may have different energy requirements than bats at lower latitudes. To evaluate the extent of these differences, we estimated an energy budget and refueling rates for reproductively active female little brown bats (*Myotis lucifugus*) roosting in buildings in eastern Alaska (~63°N). Physiological parameters (torpor use and metabolic rates) and daily energy expenditures ($25.7 \pm 5.3 \text{ kJ d}^{-1}$) were similar to, or slightly lower than, conspecifics at lower latitudes. Northern little brown bats foraged for less time than southerly conspecifics, but measurements of plasma β -hydroxybutyrate concentrations suggest that northern bats refuel at a rate considerably higher than those to the south. It appears that high refueling rates (and therefore foraging intensity) involve a dietary shift to orb-weaver spiders, which are abundant and likely offer higher energetic benefit than the small, flying insects consumed by individuals in other parts of the distribution. Environmental factors may limit species' distributions, but our results provide an example of a population at the limit of their geographic range that has compensated for environmental challenges by adopting unique behavioral strategies while the underlying physiology (including daily energy expenditure) remains similar to populations at the core of the species' range.

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1. Introduction

Widespread organisms at the edge of their species' geographic range often experience environmental conditions different from those experienced by individuals in the core of the distribution, and it is logical to expect variation in traits that help organisms respond to those

environmental conditions. Small endotherms inhabiting high latitudes serve as an interesting model for studies on physiological and behavioral traits at the extremes of a species' distribution because of the unique environmental conditions they face. Nighttime temperatures, even in mid-summer, can be cool. Long periods of daylight, or a lack of complete darkness, may inhibit foraging in nocturnal animals or expose them to diurnal predators [1,2]. Finally, short summers limit time available to prepare for the long upcoming winter, which may be harsh for animals that remain at high latitudes or may force some individuals to migrate to more favorable climates. These environmental conditions may be

* Corresponding author.

E-mail address: jgboyles@siu.edu (J.G. Boyles).

¹ Authors contributed equally.

costly for small endotherms; however, during summer at high latitudes, food may be abundant and competition low, allowing for the maintenance of a balanced energy budget.

Insectivorous bats have the added energetic cost of flight and physical limitations of carrying ingested prey while flying. During summer, little brown bats (*Myotis lucifugus*) at lower latitudes forage for 4 h or more throughout the night to meet energetic requirements of pregnancy and lactation [3–5]. However, during pregnancy and lactation, bats at high latitudes have shorter periods of true darkness for much of summer [1]. After the reproductive period, adults must fatten, and young must mature in time for migration and hibernation [6] before the relatively early onset of winter. Unless bats at the northern edge of the geographic range represent a population sink, they must maintain energetic balance in the face of the many challenges posed by conditions at high latitude. To survive and reproduce, these bats may either lower physiological costs (e.g., thermoregulatory costs), and/or increase nutrient intake (e.g., forage longer or more efficiently).

One of the most obvious physiological adjustments available to small mammals to maintain energy balance is the use of facultative heterothermy (e.g. torpor). When environmental conditions are unfavorable or energy availability is low, torpor can lead to substantial energy savings over maintaining euthermia [7,8]. However, torpor has other costs, and may be avoided if other options are available [9,10]. For example, torpor during pregnancy can slow fetal development [11–13] resulting in later parturition dates and decreased juvenile survival and reproductive success [14]. If bats use torpor extensively to maintain energy balance, the potential trade-off between energy conservation and fetal development may lead to an important constraint on the life history of populations at high latitudes.

We examined the energetics of one of the highest latitude bat colonies (63°N) extensively studied to date (and in fact at the extreme of the distribution for the entire order). Given the challenges of the high latitude environment, such as low ambient temperature, short or non-existent periods of darkness, short active season, and long winter duration, we hypothesized that to maintain energy balance, bats must either exhibit a physiological response to reduce energy expenditure and/or exhibit a behavioral response to increase energy acquisition. Our initial goal was to estimate a simple energy budget for little brown bats with the prediction that bats would exhibit a physiological response at northern latitudes and use torpor more frequently than bats in the core distribution for the species. Upon finding that northern bats have remarkably similar energy expenditure to bats farther south, we further investigated behavioral responses that may allow bats to increase energy acquisition, with the prediction that bats would have increased foraging intensity to compensate for the short night duration.

2. Methods and materials

2.1. Study species and sites

Our study was conducted in and around Wrangell-St. Elias National Park and Preserve, Alaska. The data presented herein detail work on a single bat colony (>300 individuals) inhabiting two nearby buildings on the Tok Cut-off Highway near Mentasta, Alaska (62.89°N, 143.68°W). Little brown bats were the only species captured, and is the only *Myotis* species recorded at this latitude in Alaska [15]. During the first year of the study (summer 2012), we held all captured bats until they defecated so that we could identify dietary items. During the second summer study period (27 June–10 July 2013), the majority of the bats were found in a public roadhouse consisting of one main building with a café and bar, and several smaller buildings that have been attached to serve as the kitchen, refrigeration units, and storage. Bats were frequently seen and heard at the various entrances, indicating that they did not always roost in the center of the building. During winter 2013–2014, the roof on the roadhouse was replaced, and nearly all of the bats evacuated the building. A large number of them were

discovered at an abandoned cabin directly across the road (~300 m away), therefore, during the third study period (summer 2015), all work was conducted around the abandoned cabin. The cabin was boarded up and locked, with no accessible human entrance, and bats exited from at least three openings.

2.2. Energy budget calculations

We estimated a simple energy budget during the reproductive period, using data obtained from skin temperature (T_{sk}) and metabolic rate measurements. Briefly, we measured T_{sk} of thirteen non-lactating adult female bats over part or all of the 14-d study period in 2013 using temperature-sensitive transmitters (0.3 g, Model A2414, Advanced Telemetry Systems, Isanti, MN) as recorded by a datalogger (Model DL-2, Lotek Wireless, Newmarket, Ontario). We estimated metabolic rates by measuring carbon dioxide production of 18 bats in a flow-through respirometry system (Sable Systems, Las Vegas, NV) at four approximate temperatures: 15, 22, 36, and 29 °C, in that order. We used an exploratory curve-fitting procedure to fit mathematical models of the relationship between ambient temperature and all euthermic metabolic rates (EMR; pools data both within and below the thermal neutral zone into a single function) and torpid metabolic rate (TMR). This method deviates slightly from the more common three-equation model often used to describe the relationship between ambient temperature and metabolic rate, but fully captures the patterns in this case while simplifying energy budget calculations. Full details on methodology we used for T_{sk} and metabolic rate data can be found in the Supplementary methods.

We used metabolic rate data to estimate energy expenditure of a 7.5 g bat (approximately the mass of bats in the metabolic experiment) based on roost temperature measurements made across the 14-day study period. We used temperature-sensitive dataloggers (iButtons, Model 1922L, Maxim Semiconductors, Dallas, TX) placed in two roost entrances to estimate roost temperature (Fig. 1). Ambient temperatures during this period ranged from above normal for this area (as high as 31.7 °C) at the beginning of the period to within normal temperatures (max temperatures < 25 °C) for the last several days.

Our methodology precluded measurements of the energetic cost of flight, so we used Speakman and Thomas' [16] allometric equation to estimate the cost of flight for a 7.5 g bat as 4.14 kJ/h. Based on gaps in the T_{sk} data when bats were out of range of the datalogger placed at the roost and bat detector data, we estimated that bats foraged for approximately 2 h during the darkest part of the night on nights when they did forage. We do not have data on night roosting, so our calculations may overestimate the cost of the period when bats were away from the roost. We calculated several different energy budgets based on different assumptions. We estimated maximal energy expenditure by assuming that bats remained euthermic at all times, as did many of the individuals in this study (see Results). We used ambient temperature (T_a) measured across the entire 14-day period for this calculation. For the four bats that used torpor at least once, we also calculated an energy budget assuming they were expending energy at the rate described by the function for torpid metabolic rate (see Results) anytime $T_{sk} < 30$ °C.

The energy budget experiments and distributional study were approved by the University of Tennessee Animal Care and Use Committee (Protocol Number 2026-0711), U.S. Department of Interior National Park Service Permit WRST-2011-SCI 0016, and Alaska Department of Fish and Game Permit 13-149.

2.3. Plasma metabolite analysis

In summer 2015, we used plasma metabolite analysis [17] to assess foraging intensity. Briefly, concentrations of certain metabolites in blood plasma change predictably with feeding. We measured β -hydroxybutyrate concentrations in blood plasma of fasted bats as they emerged from the roost to forage and from bats as they returned after

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