Interspecific variation in evaporative water loss and temperature response, but not metabolic rate, among hibernating bats

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Hibernation is widespread among mammals and is an important adaptation that allows animals to go weeks or months without food while reducing their metabolic rate to a small fraction of euthermic metabolic rate1,2. Hibernation allows animals to cope with seasonal resource limitations, and therefore affects many aspects of the biology of hibernating species. For example, physiological constraints in hibernation may contribute to defining distribution limits3. Hibernation is also associated with extreme longevity4 despite high mortality in young individuals5. Also, the seasonality of hibernation is related to reproductive patterns, leading to differences in phenology between sexes6,7. Furthermore, hibernating species may be particularly susceptible to climate change7–9. Thus, hibernation is fundamental to the ecology, life history, and conservation of many mammalian species.

Hibernation is widespread among mammals and is an important adaptation that allows animals to go weeks or months without food while reducing their metabolic rate to a small fraction of euthermic metabolic rate1,2. Hibernation allows animals to cope with seasonal resource limitations, and therefore affects many aspects of the biology of hibernating species. For example, physiological constraints in hibernation may contribute to defining distribution limits3. Hibernation is also associated with extreme longevity4 despite high mortality in young individuals5. Also, the seasonality of hibernation is related to reproductive patterns, leading to differences in phenology between sexes6,7. Furthermore, hibernating species may be particularly susceptible to climate change7–9. Thus, hibernation is fundamental to the ecology, life history, and conservation of many mammalian species.

Multi-species comparisons can reveal general patterns of physiological diversity10, including diversity within similar environments or across varied environmental contexts. However, many experimental studies of hibernation focus on a single species, and studies that experimentally compare multiple species are uncommon. Several
authors have conducted extensive literature reviews compiling information from across all heterothermic mammals, and even heterothermic birds in some cases, but interpretations can be limited by comparing studies with varying methodologies, or complicated by differences in environmental contexts. General patterns of hibernation strategies within most taxonomic groups are poorly understood. Multi-species comparisons can complement single species empirical studies and broad literature reviews.

Bats are a diverse group with species that hibernate in a wide variety of conditions. In temperate regions, hibernation enables bats to persist through extended periods of cold (thermoregulatory challenge for small-bodied endotherms with high mass-specific metabolic rates) when insect prey resources are largely absent. Therefore, bats are an ideal group for studies of interspecific variation in hibernation physiology, but most hibernation research has focused on a small number of species. The closest to a model species for bat hibernation is likely *Myotis lucifugus* e.g., but, in general, little is known about the hibernation physiology of most species.

Two key parameters for understanding hibernation physiology are torpid metabolic rate (TMR) and the rate of evaporative water loss (EWL). Hibernation consists of long periods of torpor interspersed by brief periodic arousals to euthermic body temperatures. Evaporative water loss is important for hibernating bats as thirst and dehydration may be key drivers of periodic arousals. Variation among species in these parameters may reveal differences in energetic costs of hibernation or may reflect adaptation to different environmental conditions. Many species of bats have large geographic ranges, with dramatic variation in environmental conditions across the range. In a previous study, we considered intraspecific variation in hibernation of two species (*Corynorhinus townsendii* and *Myotis lucifugus*; data included in this study). Despite large geographic distances and populations sampled from different biomes, TMR did not vary among populations and EWL was generally consistent, with some minor differences across sites. Here we expand on that research by conducting a similar comparison among species.

We tested for interspecific variation in hibernation physiology among 13 species of hibernating bats across the western United States and Canada. We sampled ecologically diverse species of hibernating bats across a large geographic range and therefore we predicted that torpid metabolic rate and evaporative water loss would vary among species. For each species we determined several important parameters reflecting different hibernation strategies: the minimum torpid metabolic rate (TMR_{min}), the temperature range over which TMR_{min} was measured, and the minimum defended temperature (T_{defended}) below which metabolic rate increased. We tested for differences among species, but from an ecophysiology perspective of seeking patterns among diverse organisms, we also tested whether species clustered into groups, reflecting a smaller number of general hibernation strategies. Alternatively, lack of clustering may indicate a broad continuum of hibernation strategies across species.

**Methods**

We collected data from 13 species of bats at 14 sites across the western United States and Canada, including sites in Northwest Territories, Alberta, British Columbia, Montana, Oregon, Utah, Nevada, Colorado, Oklahoma, and Texas (Fig. 1; Table 1). Field methods follow McGuire et al. Briefly, we visited hibernacula (abandoned
Species | n | Sites | Body mass (g) | Range tested (°C) | Temperature effect | TMRmin (mW g⁻¹) | Range TMRmin (°C) | T_defended (°C) | EWL (mg H₂O min⁻¹ g⁻¹) | EWL cluster
---|---|---|---|---|---|---|---|---|---|---
**Vespertilionidae**
*Corynorhis townsendii* | 152 | BC, CO, NV, OR, UT | 10.3 ± 0.1 | 2–10 | LRₚ = 13.0, p = 0.005 | 0.33 ± 0.03 | 5–8 | 2–5 | 0.009 ± 0.001 | Low
*Eptesicus fuscus* | 7 | MT | 16.7 ± 1.2 | 2–10 | LRₚ = 8.16, p = 0.067 | 0.25 ± 0.07 | 2–10 | <2 | 0.009 ± 0.002 | Low
*Lasionycteris noctivagans* | 23 | BC | 12.7 ± 0.2 | 0–8 | LRₚ = 15.6, p = 0.004 | 0.15 ± 0.01 | 2–8 | 0–2 | 0.005 ± 0.001 | Low
*Myotis californicus* | 27 | BC, NV | 5.0 ± 0.1 | 0–10 | LRₚ = 22.0, p < 0.001 | 0.26 ± 0.02 | 2–8 | 0–2 | 0.010 ± 0.002 | Low
*Myotis cilioluinus* | 13 | MT, NV | 7.5 ± 0.2 | 2–10 | LRₚ = 16.7, p = 0.002 | 0.48 ± 0.09 | 5–10 | 2–5 | 0.019 ± 0.001 | High
*Myotis lucifugus* | 99 | MT, AB, NWT | 8.9 ± 0.1 | 2–10 | LRₚ = 15.2, p = 0.002 | 0.30 ± 0.02 | 2–8 | <2 | 0.014 ± 0.001 | High
*Myotis thysanodes* | 11 | MT | 9.4 ± 0.3 | 2–10 | LRₚ = 11.2, p = 0.011 | 0.25 ± 0.08 | 5–10 | 2–5 | 0.018 ± 0.001 | High
*Myotis velifer* | 33 | OK | 14.4 ± 0.3 | 2–10 | LRₚ = 8.0, p = 0.046 | 0.25 ± 0.04 | 5–10 | 2–5 | 0.015 ± 0.001 | High
*Myotis volans* | 12 | MT, MT | 9.0 ± 0.2 | 2–10 | LRₚ = 10.6, p = 0.014 | 0.43 ± 0.08 | 5–10 | 2–5 | 0.015 ± 0.001 | High
*Myotis yumanensis* | 27 | BC, BC | 5.8 ± 0.1 | 0–8 | LRₚ = 48.4, p < 0.001 | 0.20 ± 0.01 | 4–6 | 2–4 | n/a² |
*Perimyotis subflavus* | 34 | OK | 7.0 ± 0.1 | 2–10 | LRₚ = 17.1, p = 0.001 | 0.18 ± 0.04 | 8–10 | 5–8 | 0.017 ± 0.002 | High

**Molossidae**
*Tadarida brasiliensis* | 27 | TX | 13.4 ± 0.4 | 2–12 | LRₚ = 63.2, p < 0.001 | 0.35 ± 0.06 | 8–12 | 5–8 | 0.010 ± 0.001 | Low

Table 1. We collected data from 13 species of hibernating bats, including metabolic rate and evaporative water loss. Torpid metabolic rate (TMR) varied across temperatures (Temperature Effect column) and the range of temperatures at which the minimum torpid metabolic rate (TMRmin) was recorded varied among species. Within that range of temperatures, TMRmin did not vary among species, but species were divided into high evaporative water loss (EWL) and low EWL clusters (see Fig. 3). Values reported as mean ± standard error. 1Subscripts identify different sites in states or provinces with multiple sites. 2Effect of temperature on metabolic rate. LR = likelihood ratio with degrees of freedom indicated in subscript. 3Where metabolic rate did not increase at coldest temperature tested, T_defended can only be determined as less than the lowest temperature tested. Otherwise T_defended is between the range of temperatures indicated. 4L. noctivagans may represent a third cluster with lower EWL (see Fig. 3b), but to be conservative we present only two clusters here. 5EWL was not measured for Myotis yumanensis.
temperature ($T_{\text{defended}}$; ambient temperature below which metabolic rate increases), minimum torpid metabolic rate ($T_{\text{MRmin}}$) and the temperature range over which $T_{\text{MRmin}}$ was measured (range over which TMR did not vary based on post-hoc comparisons). We calculated EWL from the same range of temperatures as $T_{\text{MRmin}}$.

We report mass-specific metabolic rate here for comparisons among species, but analysis of whole-animal metabolic rate results in the same qualitative results. Some of the data presented here for *C. townsendii* and *M. lucifugus* have previously been included in analysis in McGuire et al. To compare $T_{\text{MRmin}}$ and EWL among species we conducted two analyses. The temperature range of $T_{\text{MRmin}}$ varied among species, and there were repeated measurements of individuals at different temperatures within that range. Therefore, we randomly selected one measurement per individual and used linear models to test for a difference in $T_{\text{MRmin}}$ or EWL among species, repeated this process 1,000 times and used a one-tailed one sample t-test to determine whether the mean p-value was less than 0.05. We also performed a k-means cluster analysis to describe similarity among groups of species across $T_{\text{MRmin}}$ and EWL values. We did not measure EWL for *M. yumanensis* and therefore this species is excluded from the cluster analysis.

All methods at U.S. field sites were approved by the Institutional Animal Care and Use Committee at Texas Tech University (protocol 16031-05). All fieldwork in Canada conformed to guidelines of the Canadian Council on Animal Care and ethics approvals for fieldwork in Canada were provided by the respective provincial/territorial/parks agencies noted below. Permits to conduct fieldwork were approved by Alberta Environment and Parks (17-214, 18-016), British Columbia Ministry of Forests, Lands and Natural Resource Operations (MRCB15-163558), Colorado Parks and Wildlife (16TR2172, 17TR2172, 18TR2172, and 19TR2172), Montana Department of Fish, Wildlife & Parks (2016-104, 2017-018, 2018-008), National Park Service (ORCA-2018-SCI-0001), State of Nevada Department of Wildlife (497636), Northwest Territories Department of Environment and Natural Resources (WL500648), Government of Northwest Territories Wildlife Care Committee (NWTWCC 2018-015), Oklahoma Department of Wildlife Conservation (7245), Parks Canada (WB2018-020, WB-2018-28777), Texas Parks and Wildlife (SPR-0416-115), and Utah Division of Wildlife Resources (2COLL10094). Although none of our sites were affected by white-nose syndrome at the time we conducted our fieldwork, we followed recommended protocols for fieldwork and decontamination.

All statistical analyses were conducted in R v3.6.3.

### Results

The 13 species in our dataset included a range of widespread hibernators and hibernating individuals of two species not normally considered to be hibernators (*L. noctivagans* and *T. brasiliensis*). Sample sizes, sampling locations, body mass, and respirometry results are summarized in Table 1. Torpid metabolic rate varied seasonally for *C. townsendii* (slightly greater in winter, likelihood ratio = 4.38, df = 1, $p = 0.04$), but there was no seasonal effect for *M. cilolabrum*, *M. lucifugus*, *M. velifer*, or *P. subflavus* (all $p > 0.36$). We could not test for seasonality among the remaining species because of either limited sample size or because we only had data from one season. Species varied in their response to temperature; some species aroused at colder temperatures (Fig. 2a) whereas other species maintained a consistently low TMR across temperatures (Fig. 2b). The temperature range of $T_{\text{MRmin}}$ varied among species (Fig. 3a). The highest minimum defended temperature was observed for *T. brasiliensis* and *P. subflavus*. For these species, TMR increased at 5 °C, indicating a minimum defended temperature somewhere between 5 and 8 °C. Conversely, *E. fuscus*, *L. noctivagans*, *M. californicus*, *M. cilolabrum*, and *M. lucifugus* maintained $T_{\text{MRmin}}$ to < 2 °C (Fig. 3a; statistical results of temperature effects included in Table 1). When measured...
within the temperature range of \( T_{\text{MRmin}} \), EWL varied among species (\( n = 1000 \) random draws, mean linear model \( p \) value < 0.0001, one-sample \( t \) test \( t_{999} = 11,681, p < 0.0001 \)) but \( T_{\text{MRmin}} \) did not vary among species (\( n = 1000 \) random draws, mean linear model \( p \)-value = 0.12, one-sample \( t_{999} = 25.1, p > 0.99 \)). Accordingly, cluster analysis indicated either two or three groups (depending on subjective interpretation of cluster analysis sum of squares) based on evaporative water loss (Fig. 3b). *Lasionycteris noctivagans* had noticeably lower EWL than all other species and may represent a separate cluster, but we conservatively present only high and low EWL clusters here.

**Discussion**

Most previous experimental studies of hibernation physiology have focused on a single species, often one of a small number of relatively well-studied species. Our study included 13 species of bats hibernating across the western United States and Canada. Some of the species in our study have been extensively studied (e.g., *M. lucifugus* and *E. fuscus*), whereas hibernation of most species in our study has received little research attention. To encompass a potentially wider range of hibernation physiology, we also included species that may not typically be considered hibernators. Through most of their range *L. noctivagans* are long-distance migrants\(^4\), but in the Pacific northwest they are found hibernating in rock crevices and mines\(^4\). Similarly, *T. brasiliensis* populations in Texas and nearby states are renowned for migrating long-distances to overwinter in Mexico\(^4\), but the species is now recognized as a partial migrant with some individuals hibernating in Texas\(^4\). Therefore, the species included in our study encompass diversity in taxonomy, ecology, and geography.

The range of temperatures that may be preferred by each species can be inferred by their physiological responses to the range of temperatures we tested. Some species in our study tolerated temperatures (i.e., remained torpid) that approached freezing. We did not observe an increase in TMR at the coldest temperature tested (2 °C) for *M. lucifugus*, *M. ciliolabrum*, and *E. fuscus*, whereas hibernation of most species in our study has received limited research attention. To encompass a potentially wider range of hibernation physiology, we also included species that may not typically be considered hibernators. Through most of their range *L. noctivagans* are long-distance migrants\(^4\), but in the Pacific northwest they are found hibernating in rock crevices and mines\(^4\). Similarly, *T. brasiliensis* populations in Texas and nearby states are renowned for migrating long-distances to overwinter in Mexico\(^4\), but the species is now recognized as a partial migrant with some individuals hibernating in Texas\(^4\). Therefore, the species included in our study encompass diversity in taxonomy, ecology, and geography.

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The breadth of temperatures over which \( T_{\text{MRmin}} \) is maintained may reflect niche breadth and the ability of species to hibernate under a broader range of environmental conditions. Although TMR declines with decreasing ambient temperature to \( T_{\text{defended}} \) at low temperatures the decrease is relatively minor and variation among individuals in our study resulted in a range of temperatures over which we did not detect variation in TMR. Two
species in our study were notable in the breadth of the TMR\textsubscript{min} temperature range, with no evidence for increased TMR across the entire range of temperatures tested for either E. fuscus or M. ciliolabrum. However, we did not detect increased metabolic rate at the highest temperatures tested for 9 of 13 species in our study. To identify the lower defended temperature and to reduce disturbance to the study animals, we focused on colder temperatures. Future study at either a wider range of temperatures, or at warmer temperatures, will help to identify increases in TMR at warmer temperatures and potential interspecific variation in niche breadth. While T\textsubscript{defended} and the temperature range of TMR\textsubscript{min} varied among species, there was no difference in TMR\textsubscript{min} across species. If measured within the appropriate temperature range for each species, all species had similar TMR. Species that hibernate in comparatively warmer regions may be adapted to warmer temperatures (e.g., T. brasiliensis) and species that hibernate in comparatively colder regions may be adapted to colder temperatures (e.g., M. lucifugus), but each can achieve comparably low TMR within their respective temperature ranges. Across the broad geographic range of our study, winter duration varies widely, with the predicted hibernation duration ranging from >200 days in our most northern site to <75 days at our most southern site\textsuperscript{52}. Rather than variation in TMR, our results suggest that hibernating bats are more likely to cope with variation in the energetic demand of hibernation by adjusting the amount of fat stored for hibernation, and the frequency of energetically costly periodic arousals. Indeed, among the most northerly studied populations, bats have exceptionally large fat stores\textsuperscript{53} and exceptionally long torpor bouts\textsuperscript{54}.

Our analysis suggests two general hibernation strategies based on EWL. While TMR\textsubscript{min} was comparable among species, species clustered into two groups based on EWL. One group was characterized by high EWL, the other by low EWL. Phylogenetic inertia (closely related species with similar phenotypes) may partially explain differences in hibernation strategy, but our results suggest phylogeny is not likely the primary driver. For example, most Myotis species had high EWL, but species from the same genus were placed in both the high and low EWL clusters. The low EWL group included both the largest (E. fuscus) and smallest (M. ciliolabrum) species in our analysis, and therefore body size is unlikely to lead to the observed patterns (also, our analysis was based on mass-specific values controlling for body size). Similarly, temperature preference is not likely an important driver of hibernation strategy, despite greater potential evaporative water loss at warmer temperatures\textsuperscript{55}. Species in the low EWL cluster are found at both the top (T. brasiliensis) and bottom (e.g., M. californicus) of the temperature ranking (Fig. 3a). Of the two species with the highest T\textsubscript{defended} T. brasiliensis fell in the low EWL cluster while P. subflavus had high EWL. We suggest that adaptation to environmental conditions experienced across their range is the most likely factor determining which hibernation strategy is adopted by a species. Although not all species can be easily categorized as occurring in either mesic or arid habitats and hibernacula are generally poorly documented for most species\textsuperscript{56}, species that tend to be found in more mesic regions were in the high EWL group (e.g., M. lucifugus, P. subflavus), whereas species from more arid regions were in the low EWL group (e.g., C. townsendii, T. brasiliensis). Notably, while minimal, the only indication of intraspecific variation among our study sites was in EWL and not TMR\textsuperscript{57}, consistent with previous studies\textsuperscript{58,59}. Maintaining water balance is critical for survival, but differences in EWL may also affect the energetic cost of hibernation. Periodic arousals account for the large majority of the energetic cost of hibernation\textsuperscript{19} and EWL may be an important driver of arousal frequency\textsuperscript{55,60}. Consequently, differences in the energetics of hibernation among species are likely to be driven by the frequency of arousals (possibly driven by EWL) and not energetic costs during torpor bouts.

We describe two hibernation strategies, high and low EWL, but these may not be strict groupings. In our dataset, L. noctivagus had notably lower EWL than any of the other species in the low EWL group and may represent a third cluster with especially low EWL. Alternatively, hibernating species may best be represented along a continuous gradient of EWL. Future studies including additional species will reveal whether there are physiological and morphological tradeoffs that give rise to two distinct hibernation strategies, or whether unsampled species would fill in intermediate values of EWL.

Interspecific differences in hibernation strategy may be an important driver of distribution patterns, disease risk, and provide a starting point for understanding the potential impacts of climate change. Hibernating bats in North America are threatened by white-nose syndrome (WNS), an introduced fungal disease\textsuperscript{60,61}. The sites in our study had not yet been affected by WNS, but the disease is rapidly spreading into western North America. Furthermore, many of the species in our study have not yet been exposed to the fungus that causes WNS, and there is interest in predicting which species may be more or less susceptible to the disease. Some of the species in our study occur in eastern North America where WNS is widespread, but all are not equally affected\textsuperscript{52}. Notably, the species in our study that have been heavily impacted in the east (M. lucifugus, P. subflavus) clustered in the high EWL group, while the species that have been less affected (C. townsendii, E. fuscus) clustered in the low EWL group. This is consistent with the growing recognition of the importance of EWL in the impacts of WNS\textsuperscript{59,62–64}. As climate change alters environmental conditions and WNS spreads across the west, the interspecific differences in hibernation physiology that we observed will contribute to species differences in response to these threats.

Our study included data collected from field sites spread >2800 km across latitudes and >2000 km across longitudes in western North America. Conducting studies on this scale is logistically challenging but provides key insights into the physiological differences that underly differentiation among species. In the Anthropocene the landscape is rapidly changing, both literally and figuratively\textsuperscript{65}. Understanding variability in physiological limitations is critical to understanding adaptive potential and how species, assemblages, communities, and ultimately ecosystem processes will be affected by the numerous stressors they face.

Data accessibility
All supporting data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.12jm63xwg.
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Author contributions
L.P.M., S.H.O., R.K.P., C.L.L., conceived the study. L.P.M., S.H.O., R.K.P., C.L.L., and C.K.R.W. secured funding. N.W.E., C.G.H., K.A.S., Y.A.D., C.L.L., and B.J.K.–B. collected data. All authors contributed valuable discussion of the data and ideas presented here. L.P.M. analyzed the data and drafted the manuscript. All authors contributed editorial comments on the manuscript.

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**Competing interests**
The authors declare no competing interests.

**Additional information**
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