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The members of the Committee approve the dissertation of Jesse Alston presented on 17 February 2021.

Dr. Jacob Goheen, Chairperson

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Dr. Lauren Shoemaker, Outside Member

Dr. Michael Dillon

Dr. Daniel Laughlin

APPROVED:

Dr. Melanie Murphy, Director, Program in Ecology

James C. Ahern, Associate Vice Provost, Graduate Education

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Body temperatures outside narrow ranges can disrupt physiological processes, so animals frequently alter their behavior and other aspects of their ecology to avoid suboptimal thermal environments. During my dissertation research, I conducted three studies on how thermal environments shape the behavior and ecology of bats. In Chapter 1, I demonstrated that male northern long-eared bats (*Myotis septentrionalis*) selected roost trees that were larger in diameter, more decayed, and under denser canopy than other trees available on the landscape—characteristics that might influence roosts' thermal properties were unimportant. This research will inform forest management in the Black Hills of South Dakota and Wyoming. In Chapter 2, I showed that male fringed myotis (*Myotis thysanodes*) did not select roosts with specific thermal characteristics, nor did ambient temperature alter patterns of roost selection. Bats can likely modulate use of torpor to maintain a consistent level of energy expenditure over the course of a day, irrespective of ambient temperature, a finding that can inform studies of the influence of temperature on habitat selection by other heterotherms. In Chapter 3, I tested four competing hypotheses for spatio-temporal variation in body size within bat species. Spatial variation in body mass was most correlated with mean annual temperature (the mechanism historically believed to underlie Bergmann's Rule), while temporal variation in body mass was most correlated with net primary productivity. Climate change is believed to be causing reductions in body size for animals, but reductions in body size will likely be more complex than has been appreciated.

ENERGETIC DRIVERS OF BEHAVIOR AND BODY SIZE IN BATS

By

Jesse M. Alston

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and the University of Wyoming

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DEDICATION

This dissertation is dedicated to Jessi Rick, who has made my life easier (and better!) in

countless ways over the past six years. I hope she can truthfully say the same.

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I am grateful to my co-advisors, Jake Goheen and Doug Keinath, for their advice and support over the past five years. Their mentorship made me a much stronger ecologist and conservation biologist. I thank both of them for taking a chance on some guy from a college they had never heard of and very little track record of coursework in biology. Ian Abernethy, maybe most knowledgeable naturalist in Wyoming, taught me to handle bats and was a tremendous guide as I learned to be a wildlife professional. My dissertation committee members Michael Dillon, Lauren Shoemaker, and Daniel Laughlin also made my research much stronger.

During my graduate work, I worked alongside some of the best field technicians I expect to ever hire: Leandra Boodoo, Corrie (McFarland) Harrison, Lucas Olson, Josh Foust, and Emma Greene. If I hire folks this competent and talented in the future, I'll consider myself tremendously lucky. Brad Phillips, Mike Wiles, Dan Austin, and Dan Licht offered valuable support and help navigating federal bureaucracy. Pat Ortegon, Carol Pribyl, Shawn Sheen, Shannon Plumb, and Ian Worthing provided vital administrative help. Administrative staff should be paid more and treated better, particularly these five. Many people shared data that made my Chapter 3 possible—they are listed in that chapter of my dissertation. My rock star labmates (Brett Jesmer, Britt Brito, Saeideh Esmaeili, Francisco Molina, Brandon Hays, Leo Malingati, and Dedan Ngatia) provided myriad valuable insights into ecology and conservation over the past few years. I will miss our rambling conversations at Coal Creek Tap, and I hope they let me work with them in the future. I owe various debts to many folks in the University of Wyoming and greater Laramie communities, including but not limited to: Rhiannon Jakopak, Lauren Azevedo Schmidt, Casey Schmidt, Bryan Maitland, Paul Dougherty, Jason Mercer, Jerod Merkle, Richard and Chris Anderson-Sprecher,

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using some amount of torpor. For all three relationships, torpor provides energy savings (i.e., the difference between solid black and dashed gray lines), and this savings is more pronounced at colder ambient temperatures. (A) For heterotherms that use at least some torpor, energy expenditure *increases* at colder ambient temperatures because while some energy is saved from employing torpor, maintaining homeothermy at colder ambient temperatures is relatively more costly than at warmer temperatures. A heterotherm exhibiting this relationship would seek *warm* microhabitats to reduce energy use. (B) For heterotherms that use at least some torpor, energy expenditure *decreases* at colder ambient temperatures because relatively more energy is saved from employing torpor even as maintaining homeothermy at colder ambient temperatures is relatively more costly than at warmer temperatures. A heterotherm exhibiting this relationship would seek *cool* microhabitats to reduce energy use. (C) For heterotherms that use at least some torpor, energy expenditure *is stable* across a wide range of ambient temperatures because the energy saved from employing torpor matches (and thus offsets) the increase in energy expended to maintain homeothermy at colder temperatures. A heterotherm exhibiting this relationship would not benefit from seeking either warm or cool microhabitats.

Fig. 2. Four competing sets of predictions of roost selection by a heterothermic bat. Each column represents one of four sets of predictions, and each row represents a statistical relationship consistent with the predictions. In column 1, energy expenditure over the course of a day is higher in warm roosts than in cool roosts (1A). In response, bats select cool roosts to minimize energy expenditure during the day (1B). In this scenario, there should be no directional relationship between ambient temperature and roost temperature (i.e., bats always select cool roosts regardless of ambient temperature; 1C). In column 2, energy expenditure over the course

of a day is higher in cool roosts than in warm roosts (2A). In response, bats select warm roosts to minimize energy expenditure during the day (2B). In this scenario, there should be no directional relationship between ambient temperature and roost temperature (i.e., bats always select warm roosts regardless of ambient temperature; 2C). In column 3, energy expenditure peaks at intermediate roost temperatures where bats use relatively little torpor but the costs of maintaining homeothermy are relatively high (3A). In response, bats select cool roosts on cool days and warm roosts on warm days (3B) because torpor saves more energy in cool roosts than in warm roosts. In this scenario, the relationship between ambient temperature and roost temperature should be positive (i.e., bats select warmer roosts on warmer days; 3C). In column 4, energy expenditure over the course of a day is constant across roosts of all temperatures (because bats can adaptively use torpor so that roost temperatures over the course of a day have little influence on overall energy expenditure; 4A). Because energy expenditure is consistent across roosts of all temperatures, bats do not select roosts due to roost temperature (4B). In this scenario, there is no relationship between ambient temperature and roost temperature (i.e., bats never select roosts due to temperatures within roosts, regardless of ambient temperature; 4C).

Fig. 3. Scatter plot illustrating the conditional effect of daily mean ambient temperature on the total duration of bouts of torpor during the day. Each point is based on observed data and represents one day. The line represents the regression line for this relationship and the grey band represents 95% credible intervals around this line. Credible intervals for this conditional effect did not cross zero (parameter estimate: -37.4 min; 95% credible intervals: -64.0 – -12.6 min), indicating that bats spent ca. 37 minutes less in torpor per day for each additional 1˚C in daily mean ambient temperature between 0445 hrs and 2100 hrs.

Fig. 4. Results of our simulation of daily energy expenditure by fringed myotis over the range of temperatures observed in used roosts. Each point represents one day. The red points represent estimated daily energy expenditure if bats never used torpor. The blue points represent our estimate of energy expenditure over the course of a day if part of the day is spent in torpor (with the daily duration of torpor a function of daily ambient temperature). The paler points on the left side of the graph represent simulated days below the range of temperatures we observed during the telemetry portion of our study. Estimates of daily energy expenditure incorporating observed bat behaviour are steady across roosts at temperatures above ca. 15°C, especially compared to estimates of energy expenditure if bats never used torpor. The blue points in this figure correspond with Row A in Fig. 2, and are most closely matched by Fig 2.4A. Additional simulations incorporating high and low estimates for the relationship between daily ambient temperatures and daily duration of torpor are presented in Fig. A2.

Fig. 5. Kernel density plots comparing thermal characteristics within used and available roost structures: mean temperature (A), time of day at peak temperature (B), and the standard deviation of temperature (C). Blue distributions represent used roosts, while orange distributions represent available roosts. These plots illustrate the results of our binomial model of roost selection. Used roosts were slightly warmer on average than available roosts, but their distributions largely overlapped (A). Temperatures peaked slightly earlier in used roosts than available roosts, but this was a function of temperatures in warmer roosts tending to peak earlier in the day ($r = -0.19$ for the relationship between mean temperature within roost structures and time of day at peak temperature) and their distributions largely overlap (B). The standard deviation in temperatures within used roosts is very similar to the standard deviation in

temperatures within available roosts, although bats did not use the few roost structures with very high standard deviations (C). Panel A in this figure corresponds with Row B in Fig. 2, and is most closely matched by Fig. 2.4B.

Fig. 6. Scatter plot of the relationship between ambient temperature on a given day and the mean temperature within used roosts. Each point is based on observed data, and represents a roost used for one day; some roosts (n = 14) were used on multiple days and thus are represented by multiple data points on this plot. The line represents the regression line for this relationship and the grey band represents 95% confidence intervals around this line. Ambient temperature on a given day did not influence whether bats used warm or cool roosts ($p = 0.06$; $R^2 = 0.04$). This figure corresponds with Row C in Fig. 2, and is most closely matched by Fig. 2.4C.

CHAPTER 3

Fig. 1. Map of capture locations for bats included in our analyses. Our final data set included 31,303 bats sampled from 1,190 sites along a >30° gradient in latitude.

Fig. 2. Intraspecific patterns in body mass across space in 20 species of North American bats, which most strongly support the heat conservation hypothesis. In the left column, we plotted the slope for each species' relationship between body mass and the predictor variable of interest (points) and 90% credible intervals (lines). Points above the dotted line at 0 indicate species in which individual body mass increased as the variable of interest increased. Species are ordered from largest (left) to smallest (right) sample sizes. In the right column, we plotted histograms of the coefficients. Row A represents the heat conservation hypothesis, Row B represents the

critical thermal limits hypothesis, Row C represents the starvation resistance hypothesis, and Row D represents the resource availability hypothesis. Distributions centered on zero indicate no consistent effect of the variable of interest on body mass, while distributions centered asymmetrically around zero indicate directional effects. Credible intervals were truncated at the limit of the y-axis for ease of interpretability. The mean estimate of the coefficient for the effect of net primary productivity on body mass for *Myotis leibii* (4.29) was excluded from the y-axis of that graph to ease interpretability, but the 90% credible interval for that estimate crosses zero as shown in the graph. Species codes are listed in Table A1.

Fig. 3. Intraspecific patterns in body mass across time in 20 species of North American bats, which most strongly support the resource availability hypothesis. In the left column, we plotted the slope for each species' relationship between body mass and the predictor variable of interest (points) and 90% credible intervals (lines). Points above the dotted line at 0 indicate species with larger masses as the variable of interest increased. Species are ordered from largest (left) to smallest (right) sample sizes. In the right column, we plotted histograms of the coefficients. Row A represents the heat conservation hypothesis, Row B represents the critical thermal limits hypothesis, Row C represents the starvation resistance hypothesis, and Row D represents the resource availability hypothesis. Distributions centered on zero indicate no consistent effect of the variable of interest on body mass, while distributions centered asymmetrically around zero indicate consistent effects. Credible intervals were truncated at the limit of the y-axis for ease of interpretability. Species codes are listed in Table A1.

References and appendices are included with each chapter. Chapters are formatted to submit for publication as research articles in peer-reviewed journals.

Roost selection by male northern long-eared bats (*Myotis septentrionalis*) in a managed fire-adapted forest

Jesse M. Alston[a,b*], Ian M. Abernethy[b], Douglas A. Keinath[c], and Jacob R. Goheen[d]

a. Program in Ecology, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA

b. Wyoming Natural Diversity Database, University of Wyoming, Laramie, WY 82071, USA

c. Wyoming Ecological Services Field Office, U. S. Fish and Wildlife Service, Cheyenne, WY 82009, USA

d. Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA

*Corresponding author: jalston@uwyo.edu

Abstract: Wildlife conservation in multi-use landscapes requires identifying and conserving critical resources that may otherwise be destroyed or degraded by human activity. Summer day-roost sites are critical resources for bats, so conserving roost sites is a focus of many bat conservation plans. Studies quantifying day-roost characteristics typically focus on female bats due to their much stronger influence on reproductive success, but large areas of species' ranges can be occupied predominantly by male bats due to sexual segregation. We used VHF telemetry to identify and characterize summer day-roost selection by male northern long-eared bats (*Myotis septentrionalis*) in a ponderosa pine (*Pinus ponderosa*) forest in South Dakota, USA. We tracked 18 bats to 43 tree roosts and used an information-theoretic approach to determine the relative importance of tree- and plot-level characteristics on roost site selection. Bats selected roost trees that were larger in diameter, more decayed, and under denser canopy than other trees available on the landscape. Much like studies of female northern long-eared bats have shown, protecting large-diameter snags within intact forest is important for the conservation of male northern long-eared bats. Unlike female-specific studies, however, many roosts in our study (39.5%) were located in short (≤ 3 m) snags. Protecting short snags may be a low-risk, high-reward strategy for conservation of resources important to male northern long-eared bats. Other tree-roosting bat species in fire-prone forests may benefit from forest management practices that promote these tree characteristics, particularly in high-elevation areas where populations largely consist of males.

Key words: Black Hills, Chiroptera, forest management, habitat use, prescribed fire, ponderosa pine (*Pinus ponderosa*), radiotelemetry

Introduction

  Habitat degradation by humans is a leading cause of extinction and population declines of species globally (Dobson et al., 1997; Halpern et al., 2008; Hansen et al., 2013). Less than 15% of Earth's land surface falls within a protected area, and less than half of that area is free from human development, agriculture, livestock grazing, light pollution, and transportation infrastructure (Jones et al., 2018). Even in relatively intact ecosystems, land uses other than conservation of nature—such as wildfire prevention, livestock grazing, recreation, and extraction of timber and other forest products—are the norm rather than the exception. Conservation measures targeting these multi-use landscapes are thus vital for conserving species (Kremen and Merenlender, 2018).

  In multi-use landscapes, successful conservation often requires the identification of critical resources for species of conservation concern so that the supply of those critical resources can be maintained or increased. Day-roosts appear to be critical resources for many bats, providing shelter from predators and environmental stressors (Fenton et al., 1994; Solick and Barclay, 2006), communal sites for social interactions (Willis and Brigham, 2004), and secure places to raise young (Kunz, 1982). Bats spend most of their time in day-roosts, alone or in groups of up to millions of individuals, depending on sex, species, and reproductive status. Patterns of bat abundance and distribution are correlated with roost availability (Humphrey, 1975), and declines in reproductive success have been documented when pregnant or lactating bats are experimentally excluded from preferred roosts (Brigham and Fenton, 1986). Because day-roosts are so important for bats, measures to conserve roosts feature prominently in bat conservation plans. Resource managers seeking to conserve bats while managing landscapes for multiple uses benefit from knowledge that promotes bat roost conservation.

We evaluated day-roost selection by male northern long-eared bats (*Myotis septentrionalis*) in a ponderosa pine (*Pinus ponderosa*) forest in the Black Hills of South Dakota, USA. Our study population inhabits a managed fire-adapted forest at the western edge of this species' range. Northern long-eared bats inhabit much of the eastern United States and southern Canada (Caceres and Barclay, 2000), but are increasingly threatened by white nose syndrome and have been protected in the United States under the Endangered Species Act since 2015 and in Canada under the Species at Risk Act since 2014. Throughout their range, northern long-eared bats roost almost exclusively in tree cavities and under sloughing bark within intact forest (Lacki et al., 2009), and forage within forests or at forest edges (Henderson and Broders, 2008; Owen et al., 2003; Patriquin and Barclay, 2003).

At our study site and other high-elevation areas in the Black Hills, male bats are much more common than females (Choate and Anderson, 1997; Cryan et al., 2000). Sexual segregation driven by elevation or temperature is widespread among bats, and is believed to be driven by differences in energy requirements that allow males to inhabit areas that are colder or have less prey (Barclay, 1991; Ford et al., 2002; Senior et al., 2005). Male northern long-eared bats are therefore likely to occupy substantially different habitat than females, but range-wide conservation for the species is informed predominantly by studies focusing on female bats (J. Alston, unpublished data). Forest managers in male-dominated areas may therefore rely on incomplete information to conserve the majority of bats within their jurisdictions. Our study provides managers in such areas with information to appropriately guide management in male-dominated areas and supplement the existing wealth of information on female habitat use.

To evaluate factors driving roost selection, we tracked adult male northern long-eared bats to day-roosts and quantified characteristics of both used and available roost trees using

variables easily measured by forest and wildlife managers. We evaluated these data using an information-theoretic approach to select the best models from a suite of candidate models. We hypothesized that in this managed forest, bats primarily select roost trees with characteristics that promote cavity formation (e.g., tree size and amount of decay), the number of nearby roosts (e.g., plot-level tree and snag density), and thermal characteristics suitable for behavioral thermoregulation (e.g., canopy cover and orientation in relation to sunlight).

Methods

2.1. Study Area

We conducted our study during the summers of 2017 and 2018 on Jewel Cave National Monument (43˚ 45' N, 103˚ 45' W) and surrounding areas of Black Hills National Forest, 16 km west of Custer, South Dakota, USA. In this area, mean monthly summer high temperatures range between 22 – 27˚C and mean monthly summer precipitation ranges between 60 – 80 mm (Western Regional Climate Center, 2018). Open ponderosa pine forests dominate our study site, with Rocky Mountain juniper (*Juniperus scopulorum*) and quaking aspen (*Populus tremuloides*) occurring locally. In our local study area, forests form a heterogenous mosaic with northern mixed-grass prairie where a large stand-replacing fire occurred in 2000. A large cave system and several smaller caves lie underground at our study site, and there is substantial topographic relief on the landscape in the form of intersecting canyon systems and rock outcrops.

Forests in this landscape are intensively managed. Black Hills National Forest typically uses even-aged management techniques other than clear-cutting (e.g., two-step shelterwood harvest). Stand harvest rotations are 120 years on average, but selective cutting occurs at 10- to 20-year intervals to harvest mature trees and thin the understory. Aside from large severe

wildfires, the forest self-regenerates and does not require planting. Forest management on private lands generally also follow this formula but thinning intervals vary (B. Phillips, personal communication). Forests on Jewel Cave National Monument are managed for resource preservation, primarily using prescribed fire.

2.2. Capture and VHF Telemetry

We used mist nets to capture bats over permanent and semi-permanent water sources (e.g., springs, stock tanks, and stock ponds). In summer (Jun–Aug) 2017 and 2018, we netted 20 and 49 nights at 15 water sources. Mist netting sites were distributed throughout our study area, and all were in or near large burned areas and harvested areas. We opened mist nets at civil sunset and closed them after five hours and during inclement weather. We affixed VHF transmitters (0.28 g LB-2X model – Holohil Systems Ltd., Carp, ON, Canada; 0.25 g model – Blackburn, Nacogdoches, TX, USA) between the scapulae of adult male northern long-eared bats with latex surgical adhesive (Osto-Bond, Montreal Ostomy, Montreal, QC, Canada). In our study area and others in the region (Cryan et al. 2000), sex ratios are overwhelmingly male. Because patterns of roost selection can differ between male and female bats (Boland et al., 2009; Elmore et al., 2004; Hein et al., 2008; Perry and Thill, 2007), we targeted males specifically. Additionally, the roosting habits of male bats are less studied than those of females—only 2 of the 14 peer-reviewed studies on roost selection of northern long-eared bats provide data on males, and 11 out of 111 peer-reviewed studies on roost selection of cavity-roosting bats in general provide data on males (J. Alston, unpublished data). All transmitters weighed <5% of the mass of the bat (Aldridge and Brigham, 1988). We tracked bats to roosts each day transmitters were active using handheld VHF receivers (R-1000 model, Communication Specialists Inc.,

Orange, CA, USA) equipped with flexible H antennae (RA-23K model, Telonics Inc., Mesa, AZ, USA). All tracking was conducted on foot. All protocols were approved by the University of Wyoming and National Park Service Animal Care and Use Committees and met guidelines approved by the American Society of Mammalogists (Sikes et al., 2016).

2.3. Roost Characterization

To characterize roosts, we collected data for each roost and randomly sampled available roost trees in our study area. We identified available roost trees by generating a sample of 200 random points within 2.53 km (the farthest distance we located a bat roosting from its capture site during our study) of sites where we captured northern long-eared bats and selecting the nearest available roost tree at a random bearing from each point. We therefore compared used roosts to 200 available roosts. We defined available roost trees as live trees >20 cm in diameter or any dead tree with a visible defect (e.g., sloughing bark or cavities) sufficiently large for a bat to roost within. For each tree and plot, we measured characteristics that may influence roost suitability (Table 1; Table A.1). We measured vegetation characteristics at two spatial scales: 1) individual trees, and 2) a 706.86-m^2 (15-m radius) plot around the tree. We also measured topographic variables at the plot scale.

2.4. Statistical Analysis

To quantify differences between roost trees used by northern long-eared bats and the 200 randomly sampled available roost trees, we used the R statistical software environment (R Core Team, 2018) to build binomial-family generalized linear models. Because we were unable to confirm that available roost trees were never used by bats, our analyses should be interpreted

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within the context of the use-availability resource selection framework (Beyer et al., 2010; Johnson et al., 2006; Manly et al., 2007). We employed an information-theoretic approach using Akaike's Information Criterion adjusted for small sample sizes (AIC_c) to compare competing models (Burnham and Anderson, 2002) using the 'MuMIn' package (Barton, 2018). We calculated AIC_c values and model weights (w_i) for all possible combinations of a maximum of 8 predictors (one variable for each 5 observations) in our set of candidate models to prevent biased coefficient estimates and unreliable confidence interval coverage (Vittinghoff and McCulloch, 2007). Predictors with variance inflation factors (VIFs) > 10 were removed from consideration in our global model to reduce problems associated with multicollinearity (Kutner, 2005). Because no model had a w_i > 0.90, we averaged model coefficients for all models with cumulative w_i > 0.95 using the full-averaging method to obtain a final averaged model (Burnham and Anderson, 2002). Finally, we validated our averaged model using area under the receiver operating characteristic curve (AUC; Manel et al., 2001; Swets, 1988).

Results

We located 2.4 ± 0.3 (range: 1-5) roost trees per bat during our study, for a total of 44 roosts used on 59 days by 18 bats. Aside from one roost in a rock crevice, bats roosted exclusively in ponderosa pines, either in cavities or under loose bark. Thirty-six out of 43 tree roosts (83.7%) occurred in dead trees (hereafter termed "snags"). Seventeen of 43 (39.5%) roosts that we located occurred in broken-off snags ≤ 3 m in height. Bats typically roosted in the same patch of contiguous forest for the active life of the transmitter. Bats roosted 790 ± 90 m (range: 55 – 2,530 m) from the sites at which they were captured.

Our global model distinguishing used roost trees from available roost trees incorporated DBH, tree height, decay class, slope, aspect (split into two components—eastness and southness), percent bark remaining, plot tree density, plot snag density, plot canopy cover, and interaction terms between slope and eastness and slope and southness. The snag variable was removed from consideration so that no variable in the global model had a VIF >10. The global model provided an adequate fit to the data (le Cessie-van Houwelingen-Copas-Hosmer global goodness of fit test; $z = 0.805$, $p = 0.421$). Our averaged model (incorporating 104 models in our confidence set) indicated that DBH, decay class, and canopy cover were important variables (Table 2). Significant ($p < 0.05$) averaged model coefficients, confidence intervals, and scaled and unscaled odds ratios are reported in Table 3. Mean differences between used and available roost trees among our variables of interest are reported in Table 4. Predictive performance of the averaged model was very high (AUC = 0.924).

Three variables (DBH, decay class, and canopy cover) were positively related to roost selection (Fig. 1; Table 2). For each 5 cm increase in DBH, odds of selection increased by 61% (95% CI: 21-113%). Use was greater than availability at all diameters >37 cm. For each 1 unit increase in decay class, odds of selection increased by 111% (95% CI: 47-203%). Use was generally greater than availability for decay classes >2. For each additional 10% increase in canopy cover, the odds of selection increased by 126% (95% CI: 55-230%). Use was greater than availability at all canopy cover levels >19%.

Discussion

Male northern long-eared bats primarily selected roosts in trees with characteristics that promote cavity formation. At the level of individual trees, bats selected for large-diameter trees

with substantial decay. This corroborates previous work on northern long-eared bats (Jung et al., 2004; Rojas et al., 2017) and is intuitive because large trees with more decay have more roost structures (i.e., cavities and loose bark) for bats to use (Reynolds et al., 1985). This is particularly true of ponderosa pines, which can produce large amounts of resin to defend against physical injury (Kane and Kolb, 2010; Lewinsohn et al., 1991) and therefore tend to develop cavities only when they are scarred or dead. In intensively managed landscapes like the Black Hills, cavities are found overwhelmingly in snags because most trees are harvested before they reach ages at which cavities typically form.

Conservation actions targeting male northern long-eared bats should include preservation of large snags whenever possible. Our study demonstrated that male northern long-eared bats select large-diameter snags (>37 cm), and large-diameter snags also tend to remain standing longer than thinner snags (Bull, 1983; Chambers and Mast, 2014). These large-diameter snags need not be tall—short (≤ 3 m) snags are important resources for male northern long-eared bats as well. Seventeen of 43 (39.5%) roosts that we located occurred in broken-off snags ≤ 3 m in height. These are important resources and are likely more vulnerable to loss during forest management activities (particularly prescribed fire) than other potential roost trees. Snags are often intentionally removed during forest management activities because of hazards posed to forest management personnel (e.g., loggers and firefighters) and the general public. However, these short snags pose less danger to forest management personnel and the public than taller snags, and their preservation is therefore a realistic and actionable step toward bat conservation.

Of the variables we considered that may influence thermal characteristics of roosts, only canopy cover influenced roost selection significantly. Trees were more likely to be used as roosts as surrounding canopy cover increased, and use was greater than availability at all canopy cover

levels >19%. Although many snags were available within our study area in open areas burned by a severe wildfire in 2000, bats in our study rarely used those snags, instead selecting snags in the interior of forest stands with live canopy. Forty out of 43 (93.0%) roosts were within intact forest stands with live canopy, and all roosts were within 50 m of intact forest stands. Bats may prefer these areas because canopy cover creates cooler environments, but they may also simply prefer to be immediately near forested areas where they forage (Henderson and Broders, 2008; Owen et al., 2003; Patriquin and Barclay, 2003). Either way, stand-replacing fire likely poses risks to local populations of northern long-eared bats at the western edge of its range, where severe wildfire is increasingly prevalent due to climate change (Westerling et al., 2006). Clearcutting also poses risks to local populations of northern long-eared bats in these areas, even if snags are retained. Selective logging that leaves some level of canopy cover remaining would ensure that snag retention is effective for bat roost conservation.

Dynamics of regional disturbance may be important when evaluating local-scale factors that influence roost selection (O'Keefe and Loeb, 2017). The ponderosa-dominated landscape where we conducted our research is substantially different than other landscapes (i.e., deciduous and mixed forests in eastern North America) where roost selection by northern long-eared bats has been studied. Although many of the factors driving roost selection appear to be similar among areas, the processes that create roosts may be fundamentally different in different areas. Snags in ponderosa pine forests are often generated in large pulses by severe wildfire and mountain pine beetles (*Dendroctonus ponderosae*), but the long-term ramifications of these resource pulses for bats are not well understood. Severe wildfire appears to create snags that are largely unused by bats. Mountain pine beetle outbreaks may do the same if beetle-induced mortality reduces or eliminates canopy cover over large areas, or if outbreaks lead to more severe

fires. Bats may instead depend on snag-generating processes that operate at more local scales and over longer intervals to create suitable roosts.

Roost selection by bats varies by sex, age class, and reproductive condition (Elmore et al., 2004; Hein et al., 2008). Studies on roost selection generally focus on females because they tend to drive reproduction, which is required to sustain populations. However, targeting roost conservation toward females exclusively may neglect resources that are important for males. Because sex ratios can be heavily biased in some areas (Cryan et al., 2000), ignoring the needs of males could leave resources that are important for most individuals inhabiting these areas unprotected. On the other hand, designing roost conservation measures on studies of males alone will leave resources that are important for females unprotected. For example, short ($\leq$ 3 m) snags are important resources for males, but they may not be for females, which aggregate in maternity colonies that may contain over one hundred individuals and require larger cavities than largely solitary males (Perry and Thill, 2007). Resource managers seeking to conserve bats should take these sex differences into account when developing conservation plans and designing studies to inform those plans. In high-elevation areas, males may be more important than females for sustaining local populations because there are few females in those areas.

Conclusions

Forest managers require actionable knowledge to guide conservation, and our results indicate that conserving large-diameter snags within intact forest stands is one such action that can be taken to conserve male northern long-eared bats in wildfire-prone coniferous forests. Short ($\leq$ 3 m) snags in particular represent a low-risk, high-reward resource to target for preservation in male-biased, high-elevation populations of this species. For federally threatened

northern long-eared bats, conserving these snags at the western edge of their range may prevent range contraction and local extinction. Similar patterns may hold true for other cavity-roosting bat species in wildfire-prone coniferous forests, like those found throughout western North America. Further study on roost selection by male bats represents an underappreciated conservation research opportunity that may be particularly valuable for high-elevation bat populations. Although bats face danger from many threats unrelated to roosts (e.g., white nose syndrome, wind energy development, etc.), roost conservation remains an important tool for bat conservation in the face of such threats.

Data Availability

Data and R code used in analysis have been archived on *Zenodo*. They can be located using the following link: https://zenodo.org/record/2727206#.XNY-iKR7k2w.

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Figures and Tables

Table 1. Variables measured at used and available summer day-roosts of male northern long-eared bats (*Myotis septentrionalis*) in the Black Hills of South Dakota, 2017–2018.

Variable	Definition
DBH	Tree diameter at breast height (cm); measured with a diameter tape
Height	Tree height (m); measured with an electronic clinometer
Snag	Tree status (live/dead)
Decay Class	Stage of tree decay on ordinal scale from 1-9; higher values denote more decay (*sensu* Maser et al., 1979)
Bark Remaining	Bark remaining on tree trunk (%); estimated visually
Canopy Cover	Average of 4 canopy cover measurements (N/E/S/W) taken 5 m from tree (%); measured with a convex spherical densiometer
Slope	Slope of 706.9-m^2 (15-m radius) plot centered at tree (%); measured with an electronic clinometer
Tree Density	Number of live trees in 706.9-m^2 plot centered at tree
Snag Density	Number of snags in 706.9-m^2 plot centered at tree
Eastness	Difference between aspect of 706.9-m^2 plot centered at tree and 90 degrees (°); measured with a compass
Southness	Difference between aspect of 706.9-m^2 plot centered at tree and 180 degrees (°); measured with a compass
Slope*Eastness	Interaction term between slope and eastness
Slope*Southness	Interaction term between slope and southness

Table 2. Coefficient estimates in the averaged model and 95% confidence intervals. Bold variables denote significance at α = 0.05.

Variable	Estimate	LCL (95%)	UCL (95%)
Height	0.0133	-0.0767	0.1033
DBH	**0.0948**	**0.0382**	**0.1514**
Decay Class	**0.7465**	**0.3835**	**1.1094**
Bark Remaining	0.0033	-0.0113	0.0180
Snag Density	0.1010	-0.0039	0.2059
Tree Density	-0.0182	-0.0653	0.0289
Canopy Cover	**0.0816**	**0.0438**	**0.1195**
Slope	0.0323	-0.0354	0.0999
Eastness	-0.0069	-0.0207	0.0068
Southness	0.0004	-0.0041	0.0050
Slope*Eastness	0.0001	-0.0004	0.0005
Slope*Southness	0.0000	-0.0002	0.0002

Table 3. Averaged model coefficients, scaled and unscaled odds ratios (OR), and scaled lower and upper confidence limits (UCL/LCL) for significant variables.

Variable	Coefficient	Unscaled OR	Scaled OR	Units	Scaled OR LCL (95%)	Scaled OR UCL (95%)
DBH	0.0948	1.0995	1.6065	5 cm	1.2105	2.1321
Decay Class	0.7465	2.1095	2.1095	1 unit	1.4674	3.0327
Canopy Cover	0.0816	1.0850	2.2619	10%	1.5491	3.3025

Table 4. Means and standard errors for variables of interest among used and available trees.

Bold font denotes statistically significant variables in the final averaged model.

Variable	Roost		Available	
	Mean	SE	Mean	SE
Height (m)	8.53	1.11	9.01	0.43
DBH (cm)	**35.69**	**1.57**	**30.33**	**0.69**
Decay Class	**4.95**	**0.33**	**3.72**	**0.18**
Bark Remaining (%)	74.19	4.22	69.73	2.49
Snag Density	4.74	1.03	2.12	0.23
Tree Density	19.84	2.15	10.76	1.12
Canopy Cover (%)	**36.83**	**3.02**	**14.96**	**1.39**
Slope (%)	16.87	1.62	11.66	0.64
Eastness (˚)	76.36	8.21	93.35	3.81
Southness (˚)	109.48	11.14	96.58	5.48

Fig. 1. Unscaled odds ratios associated with each variable in the averaged roost selection model. Error bars represent 95% confidence intervals.
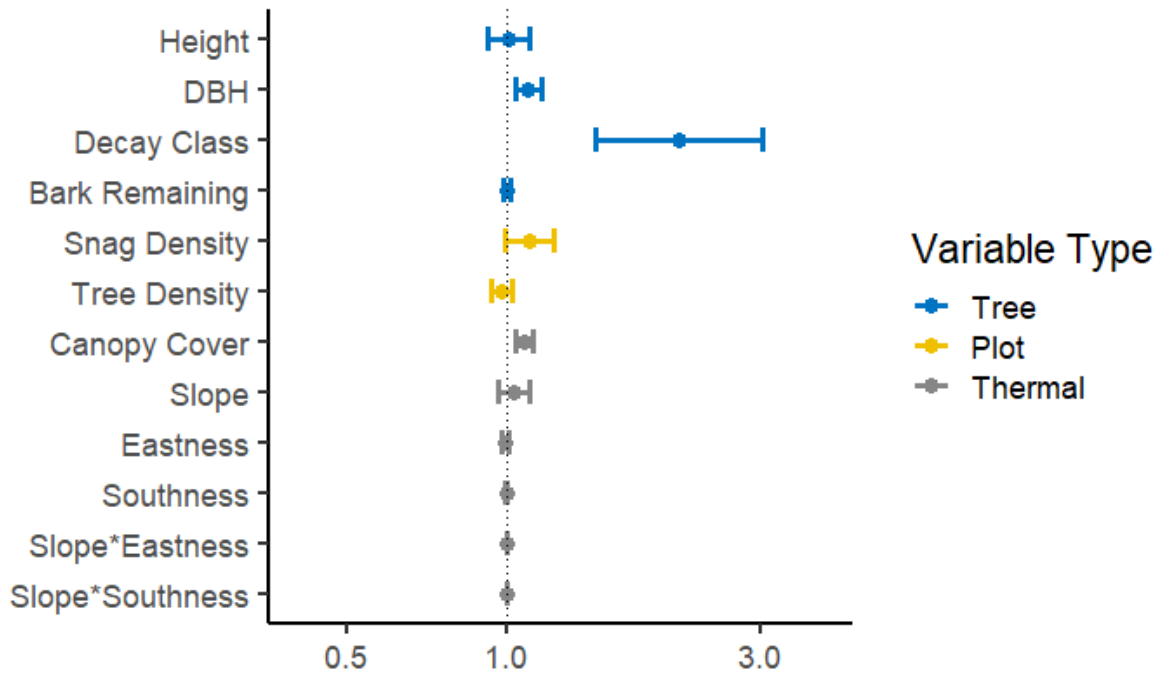
Appendix A: Supplementary Materials

Table A.1. *A priori* rationales for including variables of interest in the global model.

Variable	Rationale
DBH	Larger diameter trees are more likely to contain cavities
Height	Taller trees are more likely to contain cavities and cavities may be farther from the ground
Snag	Dead trees are more likely to contain cavities
Decay Class	More decayed trees are more likely to contain cavities
Percent Bark	Loose bark on snags may offer roost sites for bats
Canopy Cover	Increased canopy cover is likely to cool roosts below the canopy
Slope	Required for slope*aspect interactions
Tree Density	Bats may prefer roosts in areas with more potential roosts nearby
Snag Density	Bats may prefer roosts in areas with more potential roosts nearby
Eastness	Roosts on east-facing slopes will warm quicker in the morning and cool quicker in the evening
Southness	Roosts on south-facing slopes will be in direct sunlight for longer
Slope*Eastness	Steeper slopes are likely to exacerbate the effects of eastness
Slope*Southness	Steeper slopes are likely to exacerbate the effects of southness

Fig. A.1. Density plots of significant variables in the averaged model. Use was generally greater than availability at all decay classes > 2, all DBHs >37, and all canopy cover levels >19%.

CHAPTER 2
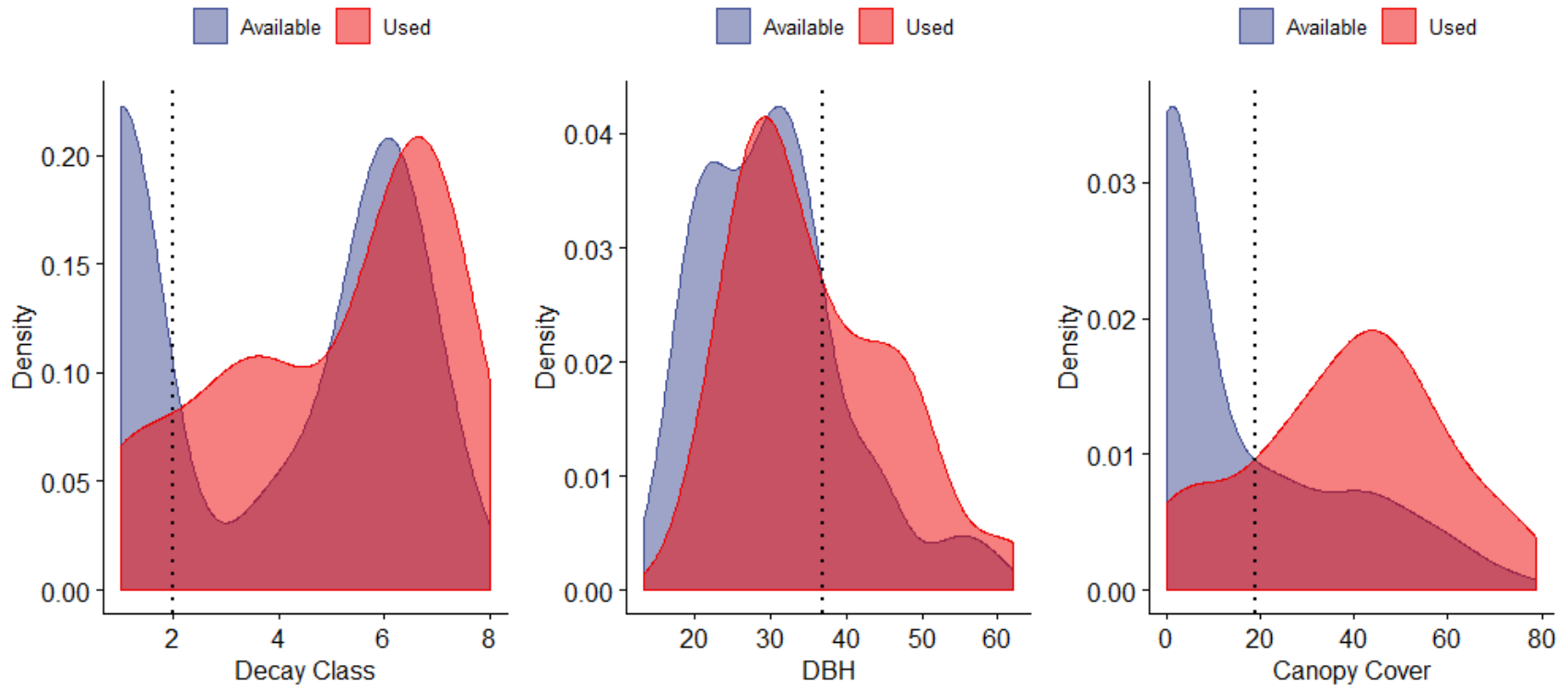
Temperature-driven use of torpor stabilizes daily energy expenditure across variable thermal conditions for a widespread bat

Jesse M. Alston[*][a,b,c], Michael E. Dillon [a,b], Douglas A. Keinath [d], Ian M. Abernethy [c], and Jacob R. Goheen [a,b]

[a] Program in Ecology, University of Wyoming, Laramie, WY, USA

[b] Department of Zoology and Physiology, University of Wyoming, Laramie, WY, USA

[c] Wyoming Natural Diversity Database, University of Wyoming, Laramie, WY, USA

[d] Wyoming Ecological Services Field Office, United States Fish and Wildlife Service, Cheyenne, WY, USA

[*] Corresponding author: jalston@uwyo.edu

Abstract

1. Many animals employ heterothermy to conserve energy during periods of inactivity, stress, or low resource availability. Unlike homeotherms, these heterotherms have some flexibility in body temperature. Unlike poikilotherms, heterotherms can maintain body temperatures somewhat independently from their environments. Heterotherms should

thus exhibit fundamentally different responses to extreme environmental temperatures than either homeotherms or poikilotherms.

2. In a species of heterothermic bat (*Myotis thysanodes*), we studied how daily torpor and roost selection could mitigate energetic consequences of variation in ambient temperature. We then (1) quantified the relationship between ambient temperature and torpor use, (2) simulated daily energy expenditure over a range of roost temperatures, and (3) quantified the influence of roost temperature on roost selection.

3. Bats did not select roosts with specific thermal characteristics, nor did ambient temperature alter patterns of roost selection. This was likely because bats could modulate use of torpor to maintain a consistent level of energy expenditure over the course of a day, irrespective of ambient temperature.

4. Thermoregulatory processes in heterotherms are likely to differ from that of homeotherms and poikilotherms, including through behaviours as universal as habitat selection. Further research on how heterotherms use daily torpor will be important for understanding the costs and benefits of this poorly understood thermoregulatory strategy.

Introduction

The thermal environments in which organisms live strongly influence metabolic rates (Huey and Stevenson 1979, Brown et al. 2004, Pörtner and Farrell 2008). Among homeotherms— which regulate body temperature internally within a narrow range to optimize physiological processes—metabolic heat production is tightly regulated in response to variation in

temperature in the surrounding environment (i.e., ambient temperature; Lowell and Spiegelman 2000). Controlling body temperature thus leads to increased energy expenditure by homeotherms when ambient temperatures depart from the thermoneutral zone (i.e., the range of ambient temperatures in which homeotherms can regulate body temperature with minimal metabolic effort; McNab 2002). Because survival and reproduction require that energy intake equal or exceed energy expenditure, operating in ambient temperatures outside the thermoneutral zone can reduce fitness over time (Angilletta et al. 2010, Boyles et al. 2011).

Although the influence of ambient temperature on metabolism in homeotherms is understood relatively well, many animals are heterotherms that can temporarily enter poikilothermy (in which body temperature tracks ambient temperature; Withers et al. 2016). Heterothermy is common among mammals and birds (Geiser, 2004; Geiser & Ruf, 1995; McKechnie & Mzilikazi, 2011; Ruf & Geiser, 2015) and can reduce energy expenditure during both hot and cold periods (Körtner and Geiser 2008, Stawski and Geiser 2012, Boyles et al. 2016, Nowack et al. 2017). As ambient temperatures depart the thermoneutral zone, heterotherms can relax internal controls on metabolism; this physiological response allows body temperature to track ambient temperature and reduce or altogether eliminate the increased energetic costs of maintaining stable body temperatures outside the thermoneutral zone (Levesque et al. 2016). Heterotherms often achieve this by entering torpor, a hypometabolic state of inactivity in which animals maintain very low body temperatures (Ruf and Geiser 2015).

The influence of ambient temperature on torpor use (and therefore energy expenditure) by heterotherms is dynamic. Heterotherms use torpor more as ambient temperatures decrease below the thermoneutral zone (Chruszcz & Barclay, 2002; Geiser & Broome, 1993; Geiser & Kenagy, 1988; Rambaldini & Brigham, 2008; Solick & Barclay, 2006), but the energetic consequences of this behavior are unclear. For a given period of time, total energy expenditure

for heterotherms depends on (1) the duration and frequency of bouts of torpor during that time frame, (2) ambient temperatures during that time frame, and (3) the difference in metabolic rates between torpor and homeothermy at a given ambient temperature. Energy expenditures might increase as ambient temperatures fall below the thermoneutral zone: even though heterotherms save energy by using torpor, such energy savings could be exceeded by the increased energetic costs of maintaining homeothermy in colder ambient temperatures (Fig. 1A). In this scenario, torpor dampens but does not completely offset increases in energy expenditure at cold ambient temperatures. Alternatively, as ambient temperatures decline, the energetic savings from torpor could exceed the increased energy expenditure necessary to maintain homeothermy (Fig. 1B). In other words, torpor more than offsets increases in energy expenditure when it is cold. Finally, it is possible that energy expenditure by heterotherms is stable through a wide range of ambient temperatures because energy savings from using progressively more torpor at progressively colder ambient temperatures perfectly compensates for increases in energy expenditure from maintaining homeothermy at colder ambient temperatures (Fig. 1C).

Such relationships between ambient temperature and energy expenditure have cascading repercussions for other aspects of an animal's life. For example, animals seeking to avoid fitness costs from extreme ambient temperatures often move to areas of the landscape with more suitable ambient temperatures (Kearney et al. 2009, Sunday et al. 2014). Animals thus often select habitats that help them maintain body temperatures near optimal levels (Huey 1991, Melin et al. 2014, Freitas et al. 2016). At ambient temperatures below the thermoneutral zone, homeotherms select areas of the landscape where they can reduce heat loss (Courbin et al. 2017, Matthews et al. 2019) or increase heat gain from the environment (Poole et al. 2016, O'Keefe and Loeb 2017). At ambient temperatures that exceed the thermoneutral zone, homeotherms select areas of the landscape where they can increase heat loss (McCann et al.

2016, Sarmento et al. 2019) or reduce heat gain from the environment (Hovick et al. 2014, Alston et al. 2020). Because it allows animals some control over their thermal environments, ecologists and evolutionary biologists have long been interested in such temperature-dependent habitat selection by which individuals can expand the range of climatic conditions that they can tolerate (Huey 1991, Morris 2011).

Temperature-driven habitat selection is less understood for heterotherms than for homeotherms, but patterns of temperature-driven habitat selection are likely to be different between animals that use these two metabolic pathways. Homeotherms have relatively fixed relationships between ambient temperature and metabolic rate, and thus often consistently select habitats to maintain optimal body temperatures with little metabolic effort (e.g., Poole et al. 2016, Courbin et al. 2017, Sarmento et al. 2019). In contrast, looser relationships between ambient temperature and metabolic rate for heterotherms may allow heterotherms to select habitats with less regard to ambient temperature, or even to prefer habitats that might be colder than ideal for homeotherms. For example, heterothermic Australian owlet-nightjars (*Aegotheles cristatus*) preferentially roost in colder, less thermally stable tree cavities, whereas homeothermic cavity-nesting birds typically select warmer, more thermally stable tree cavities (Doucette et al. 2011). Empirical data on habitat selection by heterotherms is rare, however, particularly for free-ranging animals.

Uncertainty surrounding the form and strength of relationships between ambient temperature and energy expenditure limit our understanding of temperature-driven habitat selection by heterotherms. For an animal attempting to minimize energy expenditure during periods of inactivity, each of the hypothetical relationships between energy expenditure and ambient temperature in Fig. 1 would result in a different pattern of habitat selection. A heterotherm exhibiting the relationship shown by the dashed line in Fig. 1A should select warm microhabitats to save energy, similar to homeotherms. A heterotherm exhibiting the

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relationship shown by the dashed line in Fig. 1B should select cool microhabitats to save energy, opposite of the pattern followed by homeotherms. A heterotherm exhibiting the relationship shown by the dashed line in Fig. 1C should not select microhabitats based on their thermal characteristics. This pattern of habitat selection would also diverge from the pattern followed by homeotherms. Empirical tests of the influence of ambient temperature on energy expenditure are thus needed to understand how ambient temperature drives habitat selection for heterotherms.

We sought to understand how ambient temperature influences energy expenditure, and how energy expenditure in turn influences habitat selection, in a bat that is widely distributed throughout western North America (fringed myotis, *Myotis thysanodes*). Like other bats inhabiting temperate latitudes, fringed myotis are heterotherms that are believed to select diurnal roosts to minimize energy expenditure during diurnal periods of inactivity (Sedgeley 2001, Willis and Brigham 2005, Ruczyński 2006). At temperate latitudes, temperature within roosts can vary substantially throughout the day and year, and ambient temperature influences the amount of time bats spend in torpor each day. Like other heterotherms, bats spend more time in torpor when it is cold than when it is hot (Chruszcz and Barclay 2002, Solick and Barclay 2006, Rambaldini and Brigham 2008). We hypothesized that differences in energy expenditure at roosts of varying temperatures would drive patterns of roost selection. Specifically, we weighed evidence for four competing sets of predictions (Fig. 2).

Prediction Set 1: Bats select cool roosts regardless of ambient temperature. In this scenario, energy expenditure during the day should be higher in warm roosts than in cool roosts (Fig. 2.1A) because the energetic benefits from spending more time in torpor outweigh the energetic costs of being colder when bats are maintaining homeothermy. If this is the case, bats should select roosts that are cooler compared to available structures on the landscape (Fig. 2.1B); this

pattern of selection should be consistent regardless of ambient temperature during the day (Fig. 2.1C).

Prediction Set 2: Bats select warm roosts regardless of ambient temperature. In this scenario, energy expenditure during the day should be higher in cool roosts than in warm roosts (Fig. 2.2A) because the energetic benefits from being warmer when bats are maintaining homeothermy outweigh the energetic costs of spending less time in torpor. If this is the case, bats should select roosts that are warmer compared to available structures on the landscape (Fig. 2.2B); this pattern of selection should be consistent regardless of ambient temperature during the day (Fig. 2.2C).

Prediction Set 3: Bats select cool roosts on cool days and warm roosts on warm days (shifting roost selection). In this scenario, energy expenditure is lower in cool roosts than in warm roosts on cool days, lower in warm roosts than in cool roosts on warm days, and consistently higher in roosts at intermediate ambient temperatures (Fig. 2.3A). This may arise because of threshold effects from a non-linear relationship between ambient temperature and torpor use. Namely, a threshold may exist above which homeothermy requires relatively little energy even as bats spend little time in torpor, but below which bats save a substantial amount of energy by using torpor. Near the threshold, however, bats may use relatively little torpor even as maintaining homeothermy is relatively energetically costly. In this case, bats should select roosts that are roughly the same temperature on average as available structures on the landscape (though the distribution may be bimodal; Fig. 2.3B), and temperatures in roosts should be positively correlated with ambient temperature (Fig. 2.3C).

Prediction Set 4: Bats do not alter roost selection as ambient temperatures change. In this scenario, energy expenditure during the day is roughly equal across roosts of all temperatures (Fig. 2.4A). This could occur if bats modulate use of torpor so precisely that roost temperatures over the course of a day have little influence on overall energy expenditure. In this case, bats

should select roosts that are similar in temperature to available structures on the landscape (Fig. 2.4B), and this pattern of selection should be consistent regardless of ambient temperature during the day (Fig. 2.4C).

Materials and methods

2.1 Study Area and Species

We conducted our study during the summers of 2017 and 2018 on Jewel Cave National Monument (43˚ 45' N, 103˚ 45' W) and surrounding areas of Black Hills National Forest in South Dakota, USA. Our study area is described in Alston, Abernethy, Keinath, & Goheen (2019). Mean monthly summer high temperatures range between 22 – 27˚C and mean monthly summer precipitation ranges between 60 – 80 mm (Western Regional Climate Center 2018). Open ponderosa pine (*Pinus ponderosa*) forests dominate, with Rocky Mountain juniper (*Juniperus scopulorum*) and quaking aspen (*Populus tremuloides*) occurring locally. Forests are actively managed to prevent wildfire, and those managed by the US Forest Service and private landowners also undergo intensive logging. Forests form a mosaic with northern mixed-grass prairie where a large stand-replacing fire occurred in in 2000. A large system of caves and several smaller caves lie underground, and the landscape exhibits substantial topographic relief in the form of intersecting canyon systems and rock outcrops.

Fringed myotis roost in caves, mines, rock crevices, tree cavities, and under the sloughing bark of dead trees, and forage in forest canopy and riparian areas (O'Farrell and Studier 1980). We chose to focus on males because sex ratios of bats in the Black Hills are heavily (>90%) male-biased (a common pattern in high-elevation areas; Barclay, 1991; Cryan, Bogan, & Altenbach, 2000; Senior, Butlin, & Altringham, 2005), because male *M. thysanodes* usually roost solitarily (O'Farrell and Studier 1980), and because male bats

maintain consistent patterns of torpor use throughout the reproductive season (unlike females, which alter patterns of torpor use at different stages of reproduction; Chruszcz & Barclay, 2002; Dzal & Brigham, 2013; Johnson & Lacki, 2014).

2.2 Capture and VHF Telemetry

We used mist nets to capture bats over permanent and semi-permanent water sources (e.g., springs, stock tanks, and stock ponds). From June through August of 2017 and 2018, we netted 20 and 49 nights, respectively, at 15 water sources. We opened mist nets at civil sunset and closed them after five hours or during inclement weather.

We affixed temperature-sensitive VHF transmitters (LB-2XT model .28/.33 g – Holohil Systems Ltd., Carp, ON, Canada) between the scapulae of adult male fringed myotis with latex surgical adhesive (Osto-Bond, Montreal Ostomy, Montreal, QC, Canada). The transmitters measure and transmit data on skin temperature—an accurate proxy for body temperature—of bats, enabling researchers to delineate bouts of torpor (Barclay et al. 1996, Chruszcz and Barclay 2002, Stawski and Geiser 2010). All transmitters weighed <5% of the mass of the bat (Aldridge and Brigham 1988). We tracked bats to roosts each day transmitters were active, and installed VHF data loggers (SRX800-D1 – Lotek Wireless Inc., Newmarket, ON, Canada) that collected and recorded data transmitted by the VHF transmitters. All protocols were approved by the University of Wyoming and National Park Service Animal Care and Use Committees and met guidelines approved by the American Society of Mammalogists for research on wild mammals (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016).

2.3 Energetic Modelling

To quantify torpor use, we delineated bouts of torpor from data logger readings that captured full days (i.e., from roost entry in the morning to roost exit in the evening) of skin temperature data from individual bats. This was a fraction of total days in which we located roosts, because bats typically were not located until after they entered roosts. We defined torpor as beginning when skin temperature dropped below the lowest skin temperature of bats maintaining homeothermy during a day and ending when skin temperature began a steep rise that led to bats re-entering homeothermy or leaving a roost (as recommended by Barclay, Lausen, & Hollis, 2001; Fig. A1). Because fat reserves and body mass can substantially alter the amount of time spent in torpor (Wojciechowski et al. 2007, Stawski and Geiser 2010, Vuarin et al. 2013), we also controlled for the body mass of each individual at time of capture on torpor duration. We then used the modelling software 'Stan' (Carpenter et al. 2017) via the R package 'brms' (Bürkner 2017) to build a linear Bayesian hierarchical model to quantify the influence of ambient temperature and body mass on torpor duration while accounting for non-independence among data points collected from the same individual. The model included 3 chains run for 13,000 iterations (1,000 iterations of warm-up and 12,000 iterations of sampling). We assessed chain convergence using $\hat{R}$ and precision of parameter estimation using effective sample size. We used leave-one-out cross validation to check model fit using the R packages 'loo' (Vehtari et al. 2017) and 'bayesplot' (Gabry et al. 2019) to visually assess the cross-validated probability integral transform.

To quantify energy expenditure in bats, we combined published estimates of metabolic rates of fringed myotis as a function of temperature (Studier and O'Farrell 1976) and the linear model of the influence of ambient temperature on torpor use to simulate the influence of roost temperature on energy expenditure. Specifically, we simulated minute-by-minute energy expenditure by bats in each used roost between 0445 hrs and 2100 hrs (typical entry and exit times for bats in our study) on each day over the duration of our study period. We modeled

torpor use as a function of decision rules that reflect torpor use observed over the course of our study (raw data presented in Table A1). Specifically, we assumed that bats entered torpor immediately upon entering roosts, exited torpor after an interval determined by roost temperature, and remained in homeothermy for the rest of the time spent in the roost except for a shorter bout of torpor in the evening. We further assumed that bats would use 87% of the duration of daily torpor in the morning and 13% in the afternoon unless the afternoon bout of torpor would be less than 30 minutes in duration, in which case 100% of the day's torpor would occur in the morning period. We also assumed that the mean duration of torpor that we observed would be used in the baseline "average" roost, with the duration of torpor in warmer and cooler roosts determined by the slope of the modeled relationship between ambient temperature and torpor use described in the above paragraph. To simulate uncertainty in our estimate of the slope of the relationship between ambient temperature and daily torpor use, we repeated our simulation while replacing the mean slope estimate for the relationship between ambient temperature and torpor duration with the 2.5% and 97.5% credible intervals of that relationship.

2.4 Roost Characterization

To characterize rock roost structures, we collected data for 31 roosts located by tracking 12 bats via VHF telemetry and 62 randomly sampled available (i.e., unused by bats in our study) roosts. Hereafter, we distinguish between 'used roosts' and available but unused 'available roosts'; we use the term 'roost structure' when we refer to both used and available roosts simultaneously. We identified available rock roosts in two ways: at each used roost, we 1) located the nearest rock crevice large enough to hold a bat, and 2) generated a paired point in a random cardinal direction a random distance between 100 – 300 m away, then located the nearest rock crevice large enough to hold a bat.

To characterize tree roost structures, we collected data for 9 used roosts and 36

randomly sampled available roosts. We identified available tree roosts in two ways: at each

used roost, we 1) located the nearest snag and selected the nearest cavity large enough to hold

a bat, and 2) generated a paired point in a randomly determined distance between 100 – 300

m away, in a randomly-determined (cardinal) direction, then located the nearest tree cavity

large enough to hold a bat. For each available point, we placed data loggers in two locations:

one in a cavity in the trunk and one underneath sloughing bark. We defined available roost

trees as any dead tree with a visible defect (e.g., sloughing bark or cavities) sufficiently large

to hold a bat. This description fit every tree in which we found a bat roosting.

In Summer 2018, we monitored temperatures within both used and available roosts

using data loggers (Model MX2201; Onset Computer Corporation, Bourne, MA, USA). The

first data loggers were deployed on 17 July 2018, and the last data logger was removed on 8

October 2018. This period of time includes the full range of daily high temperatures

occurring during the active season for bats at our study site. During data logger deployment

and opportunistically thereafter, we checked roost structures for the presence of bats. We

sometimes found bats in used roosts, but we never found bats in available roosts. When we

found bats in used roosts, we waited to deploy data loggers until there was no bat within the

roost.

To quantify the thermal characteristics of each roost structure, we calculated the mean

temperature within each roost structure for periods between 0445 and 2100 hrs, which

corresponds with the period in which a bat is likely to be within a roost (Table A1). To control

for potential confounding variables, we also calculated the timing of the peak temperature in

all roost structures (because if two roost structures have the same mean temperature but peak

in temperature at different times, the roost structure with the later peak will have cooler

temperatures in the morning when bats use torpor most), and the standard deviation of

temperature during the day (because stability in roost temperature can be an important factor in roost selection; Sedgeley, 2001). To quantify the timing of the daily temperature peak, we located the peak temperature in each roost structure for each day and calculated the mean time of day at which this occurred over our study period. To quantify thermal stability in roost structures, we calculated the standard deviation of temperatures between 0445 and 2100 hrs in each roost structure for each day and calculated the mean daily standard deviation over our study period. To ensure consistency, we only calculated these values for the period between July 28 and September 31 (a period in which all data loggers were actively logging temperatures, and in which average daily high temperatures correspond with the range a bat might be exposed to during the active season in our study area).

We used the R statistical software environment (R Core Team 2020) to quantify differences between used and available roosts. To determine whether bats select cooler roosts than those available, we used the modelling software 'Stan' (Carpenter et al. 2017) via the R package 'brms' (Bürkner 2017) to build a binomial-family Bayesian model to quantify the influence of mean temperature within roost structures, the timing of daily peaks in temperature within roost structures, and the standard deviation of temperatures within roost structures on roost selection. The model included 3 chains run for 13,000 iterations (1,000 iterations of warm-up and 12,000 iterations of sampling). We assessed chain convergence using the Gelman-Rubin diagnostic ($\hat{R}$) and precision of parameter estimation using effective sample size. $\hat{R} < 1.01$ and effective sample sizes $> 10,000$ represent acceptable convergence and parameter precision (Gelman et al. 2013, Kruschke 2015). We checked predictive performance with receiver operating curve analysis using the R package 'pROC' (Robin et al. 2011) and used the R package 'bayesplot' (Gabry et al. 2019) to visually assess binned residual plots.

Results

We tracked 46 bats to 107 roosts (93 in rocks and 14 in trees) and collected 27 full days of skin temperature data from 7 bats. Data from 16 data loggers within roost structures (3 used rock, 12 available rock, 1 available tree) could not be collected because they were not relocated or were dislodged from roost structures. We thus excluded these data from analyses, leaving a total of 122 (78 rock, 44 tree) data loggers that collected data on temperatures within roost structures.

Use of torpor stabilized daily energy expenditure across the range of roost temperatures observed in our telemetry study. In our model of the effect of ambient temperature on daily torpor duration, 95% credible intervals for the effect of mean ambient temperature over the course of the day on daily torpor duration did not cross 0 (parameter estimate: -37.4 min; 95% credible intervals: -64.0 – -12.6 min), indicating that bats spent ca. 37 minutes less in torpor per day for each additional 1°C in daily mean ambient temperature between 0445 hrs and 2100 hrs (Fig. 3). Assessment of the cross-validated probability integral transform indicated that model fit was adequate. When incorporated into our simulation of bat energy expenditure over the course of a typical day, this estimate of the relationship between ambient temperature and torpor use led to similar estimates of energy expenditure across temperatures within used roosts (Fig. 4; blue points). Daily energy expenditure was roughly equivalent in all roosts with mean daily roost temperatures above 15°C. As the slope of the relationship between ambient temperature and time spent in torpor steepens, maximum energy expenditure occurs at progressively warmer temperatures and energy expenditure declines more steeply at cold temperatures (Fig. A2.A). Conversely, and as the slope of the relationship between ambient temperature and torpor flattens, maximum energy expenditure occurs at cooler temperatures and energy expenditure declines gradually at warmer temperatures (Fig. A2.B). Variation in the effect of the relationship between ambient temperature and torpor was thus greater for

colder roost temperatures—energy expenditure at warmer roost temperatures was more stable across roost temperature scenarios. Our estimates for energy expenditure using observed bat behaviour were always substantially lower and substantially less variable than our estimates for energy expenditure if bats had remained in homeothermy all day (Fig. 4; red points). Bats that remain in homeothermy would expend substantially more energy in cool roosts than in warm roosts.

Overall, temperatures in both rock and tree roost structures were similar, though roost structures in trees were slightly cooler and less stable than roost structures in rocks. During the day, rock crevices averaged 20.2˚C (range: 16.5˚ – 24.2˚C) while tree roost structures averaged 18.8˚C (range: 16.1˚ – 25.5˚C). Mean daily maximum temperatures within rock crevices were 26.1˚C (range: 17.9˚ – 40.8˚C), while mean daily maximum temperatures within tree roost structures were 28.3˚C (range: 21.0˚ – 52.1˚C). Temperatures within rock crevices peaked at 1441 hrs on average (range = 1005 – 1742 hrs), while temperatures within tree roost structures peaked at 1357 hrs on average (range = 1056 – 1659 hrs). Ambient temperature strongly influenced temperatures within roost structures. Temperatures within rock crevices at each hour (in ˚C) followed the equation 7.67 + 0.73*ambient temperature (R^2 = 0.54), while temperatures within tree roost structures at each hour followed the equation 1.63 + 1.00*ambient temperature (R^2 = 0.63). We pooled rock and tree roost structures in roost selection analyses, but we report descriptive statistics for each type of roost structure in Appendix 1.

Despite substantial variation in temperatures among roost structures, we found little evidence that the thermal characteristics of used roosts differed from those of available roosts (Fig. 5). In our model of roost selection, 95% credible intervals for the effect of mean ambient temperature over the course of the day on roost selection did not cross 0 (parameter estimate: 0.30; 95% credible intervals: 0.04 – 0.58), indicating that bats were more likely to roost in

warm roost structures than cool ones. However, predictive performance was poor (AUC: 0.650), and overall, used roosts (20.1˚C) had similar mean temperatures as available roosts (19.4˚C; Fig. 5A). Bats also did not differentiate between roost structures with temperatures peaking late in the day versus roost structures with temperatures peaking early in the day (Fig 5B). In our model of roost selection, 95% credible intervals for the effect of the timing of daily peaks in temperature on roost selection crossed 0 (parameter estimate: -0.10; 95% credible intervals: -0.34 – 0.14). Overall, used roosts (1408 hrs) had similar timing of peak temperature as available roosts (1434 hrs). Bats also did not differentiate between roosts with stable temperatures and those with more variable temperatures (Fig. 5C). In our model of roost selection, 95% credible intervals for the effect of standard deviation in roost temperature over the course of the day on roost selection crossed 0 (parameter estimate: -0.20; 95% credible intervals: -0.47 – 0.06) Overall, there was no difference in the standard deviation of temperatures of used roosts (7.0˚C) and available roosts (7.0˚C). Finally, there was also no relationship between ambient temperature on a given day and mean temperatures within roosts used on that day ($R^2 = 0.03$; $p = 0.132$; Fig. 6).

Discussion

The thermal environments in which animals operate strongly influence physiological processes, and can thereby pose substantial challenges to animals living in variable environments. How animals overcome these challenges is a central question in animal ecology. Attempts to address this question have focused largely on poikilotherms and homeotherms. Because heterotherms are neither as strongly tied to narrow ranges of body temperature as homeotherms nor as subject to ambient temperatures as poikilotherms, heterotherms are likely to respond to heat and cold fundamentally differently than either homeotherms or poikilotherms.

We sought to better understand how variation in ambient temperature influences use of daily torpor and habitat selection for heterotherms, using a species of bat as a model system. Simulations of energy expenditure at varying roost temperature indicated that bats can modulate use of torpor to maintain a consistent level of energy expenditure over the course of a day over a wide range of thermal conditions. As a result, roost selection was not driven by temperatures within roosts. Our results provide evidence for the hypothesis of no selection, detailed in Prediction Set 4 in our introduction (Fig. 2).

The energetic savings associated with torpor—particularly at cooler temperatures—likely result in habitat selection that differs substantially from habitat selection by homeotherms. For example, we showed that use of daily torpor can reduce the energetic costs of inhabiting roosts that are colder than optimal for homeotherms. If bats were strict homeotherms, the energetic costs of inhabiting cool roosts would have been substantially higher (Fig. 4), which would likely result in bats selecting warm roosts. Heterothermic bats face much less pressure to select warm habitats than if they were homeotherms, especially on colder days.

Individual traits (e.g., sex, age, and reproductive condition) may alter the energetic costs and benefits of using torpor for heterotherms, thereby driving the extent to which habitat selection might follow the pattern demonstrated in this study. For example, roost selection by bats varies by sex, age, and reproductive condition (Elmore et al. 2004, Hein et al. 2008). While male bats in our study did not select roosts with specific thermal characteristics, female bats seem to prefer warmer roosts than males while raising young and typically aggregate in social maternity colonies rather than roosting solitarily (Hamilton and Barclay 1994, Kerth et al. 2001, Ruczyński 2006). Compared to males, then, roost selection by females will likely be governed more strongly by thermal characteristics (though social thermoregulation via huddling can influence thermal conditions within roosts more than a roost's physical and

environmental characteristics; Pretzlaff, Kerth, & Dausmann, 2010; Willis & Brigham, 2007). Further research on the roles of sex, age, and reproductive condition on torpor use in heterotherms (and thus habitat selection by heterotherms) is likely to reveal important context for our findings.

Climate warming increases energy expenditure for many animals, including both poikilotherms (Pörtner and Knust 2007, Dillon et al. 2010) and homeotherms (Humphries et al. 2002, Şekercioğlu et al. 2012, Albright et al. 2017). However, the degree to which climate warming will impact heterotherms is poorly understood, largely due to a lack of data on relationships between ambient temperature, torpor use, and thermolability that is needed to accurately model the influence of ambient temperature on heterotherm metabolism (Levesque et al. 2016). Our results indicate that temperature-dependent use of torpor may stabilize energy expenditure, and thus buffer against the energetic costs associated with variable ambient temperatures. However, most of the energetic savings derived from heterothermy arise during periods of cold. Increased temperatures due to climate change may thus reduce the relative energetic benefits of heterothermy compared to homeothermy, as homeotherms experience fewer and milder periods of cold.

In conclusion, we showed that a heterothermic bat selected neither warm nor cool roosts, likely because bats can modulate torpor use to stabilize energy expenditure over the course of a day. Unlike homeotherms, bats face little pressure to select warm habitats to avoid heat loss during periods of inactivity—when maintaining a high, stable body temperature becomes energetically costly, bats can enter torpor to reduce energy expenditure. Although such fine-tuning of torpor use to stabilize daily energy expenditure is intuitive, it has not been demonstrated in previous studies to the best of our knowledge. Furthermore, our study provides evidence that the thermoregulatory behaviours of heterotherms are likely to diverge in

meaningful ways from those of homeotherms, including in behaviours as basic and pervasive as habitat selection.

Acknowledgements

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Figures and Tables

Fig. 1. Three hypothetical relationships outlining the potential energetic benefits for an individual of using torpor at cool ambient temperatures. Each hypothetical relationship would result in different patterns of habitat selection for animals seeking to minimize energy expenditure during periods of inactivity. Solid black lines (which are identical across all three panels) indicate energy expenditure over a unit of time while maintaining homeothermy 100% of the time. The dashed grey lines indicate energy expenditure over the same unit of time while using some amount of torpor. For all three relationships, torpor provides energy savings (i.e., the difference between solid black and dashed gray lines), and this savings is more pronounced at colder ambient temperatures. (A) For heterotherms that use at least some torpor, energy expenditure *increases* at colder ambient temperatures because while some energy is saved from employing torpor, maintaining homeothermy at colder ambient temperatures is relatively more costly than at warmer temperatures. A heterotherm exhibiting this relationship would seek *warm* microhabitats to reduce energy use. (B) For heterotherms that use at least some torpor, energy expenditure *decreases* at colder ambient temperatures because relatively more energy is saved from employing torpor even as maintaining homeothermy at colder ambient temperatures is relatively more costly than at warmer temperatures. A heterotherm exhibiting this relationship would seek *cool* microhabitats to reduce energy use. (C) For heterotherms that use at least some torpor, energy expenditure *is stable* across a wide range of ambient temperatures because the energy saved from employing torpor matches (and thus offsets) the increase in energy expended to maintain homeothermy at colder temperatures. A heterotherm exhibiting this relationship would not benefit from seeking either warm or cool microhabitats.
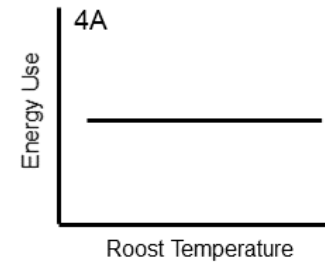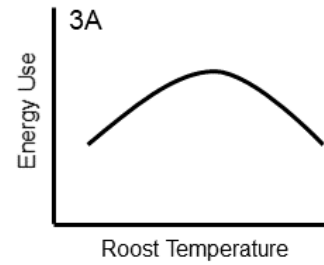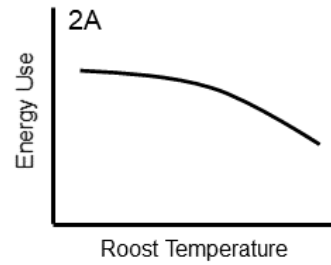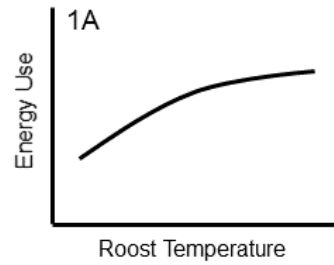
Fig. 2. Four competing sets of predictions of roost selection by a heterothermic bat. Each column represents one of four sets of predictions, and each row represents a statistical relationship consistent with the predictions. In column 1, energy expenditure over the course of a day is higher in warm roosts than in cool roosts (1A). In response, bats select cool roosts to minimize energy expenditure during the day (1B). In this scenario, there should be no directional relationship between ambient temperature and roost temperature (i.e., bats always select cool roosts regardless of ambient temperature; 1C). In column 2, energy expenditure over the course of a day is higher in cool roosts than in warm roosts (2A). In response, bats select warm roosts to minimize energy expenditure during the day (2B). In this scenario, there should be no directional relationship between ambient temperature and roost temperature (i.e., bats always select warm roosts regardless of ambient temperature; 2C). In column 3, energy expenditure peaks at intermediate roost temperatures where bats use relatively little torpor but the costs of maintaining homeothermy are relatively high (3A). In response, bats select cool roosts on cool days and warm roosts on warm days (3B) because torpor saves more energy in cool roosts than in warm roosts. In this scenario, the relationship between ambient temperature and roost temperature should be positive (i.e., bats select warmer roosts on warmer days; 3C). In column 4, energy expenditure over the course of a day is constant across roosts of all temperatures (because bats can adaptively use torpor so that roost temperatures over the course of a day have little influence on overall energy expenditure; 4A). Because energy expenditure is consistent across roosts of all temperatures, bats do not select roosts due to roost temperature (4B). In this scenario, there is no relationship between ambient temperature and roost temperature (i.e., bats never select roosts due to temperatures within roosts, regardless of ambient temperature; 4C).
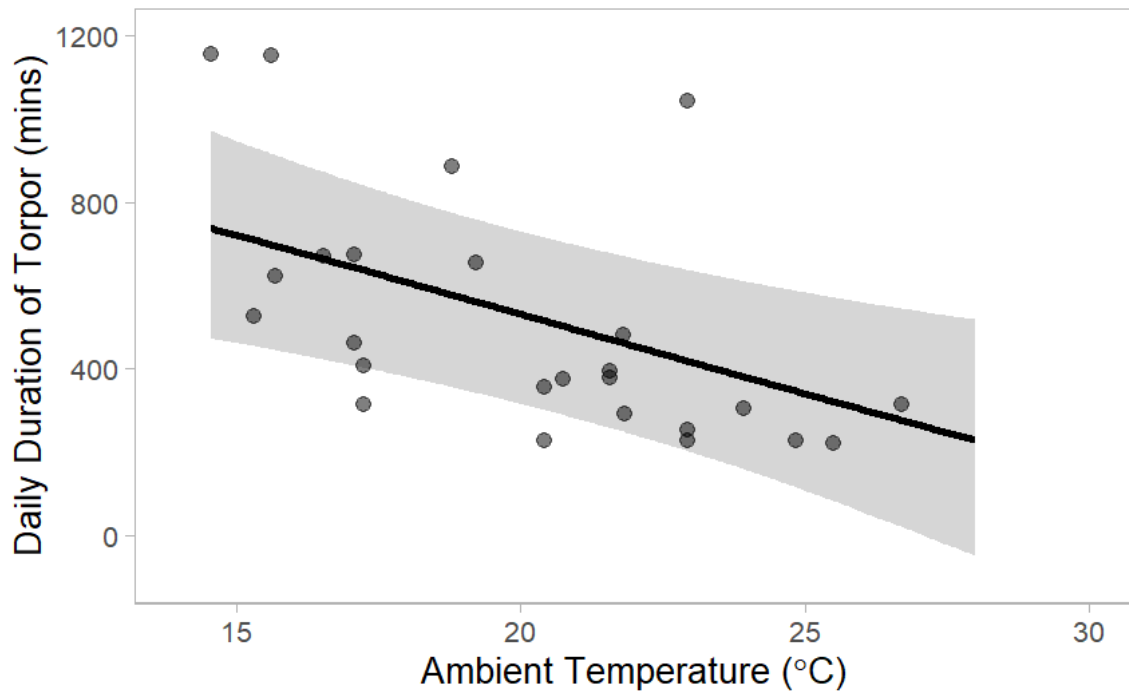
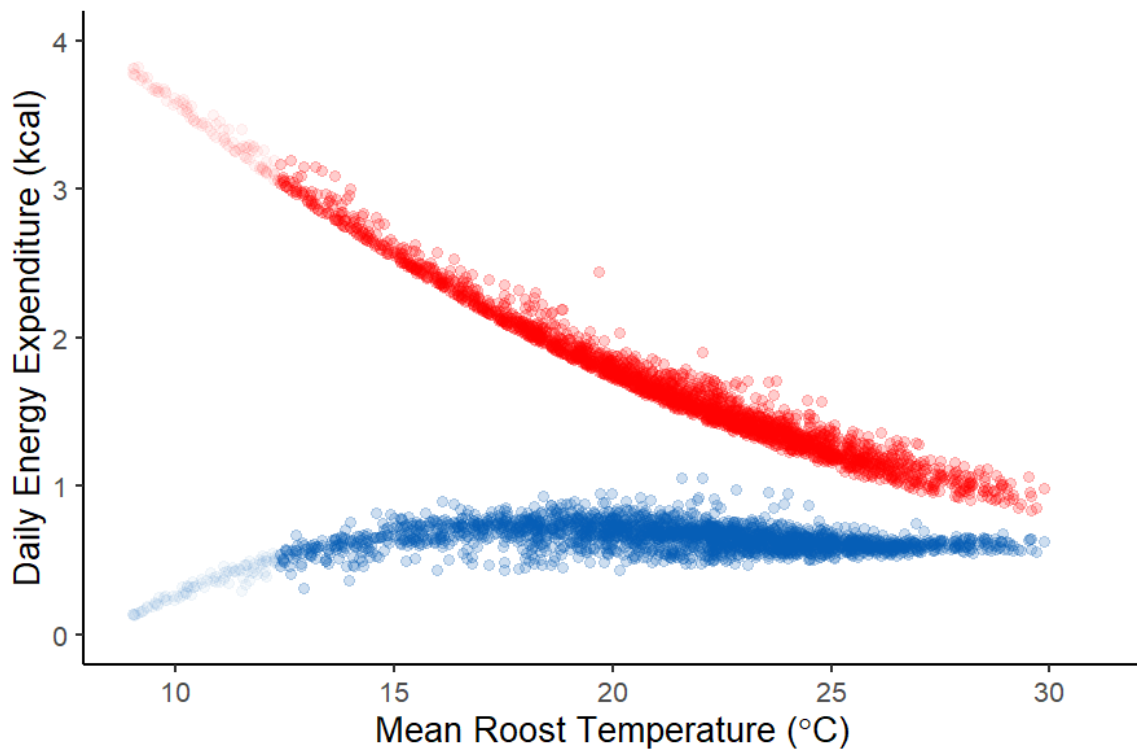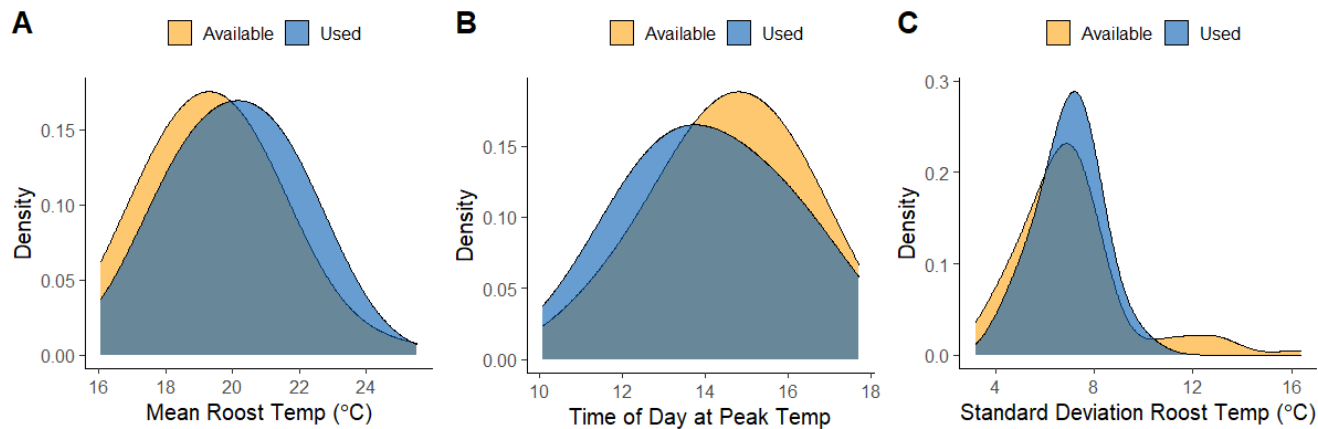| 1 \| Selection for cool roosts | 2 \| Selection for warm roosts | 3 \| Shifting roost selection | 4 \| No roost selection |

1A Energy Use / Roost Temperature

2A Energy Use / Roost Temperature

3A Energy Use / Roost Temperature

4A Energy Use / Roost Temperature

1B Probability Density / Roost Temperature — Used, Available

2B Probability Density / Roost Temperature — Available, Used

3B Probability Density / Roost Temperature — Used, Available

4B Probability Density / Roost Temperature — Used, Available

1C Roost Temperature / Ambient Temperature

2C Roost Temperature / Ambient Temperature

3C Roost Temperature / Ambient Temperature

4C Roost Temperature / Ambient Temperature

Fig. 3. Scatter plot illustrating the conditional effect of daily mean ambient temperature on the total duration of bouts of torpor during the day. Each point is based on observed data and represents one day. The line represents the regression line for this relationship and the grey band represents 95% credible intervals around this line. Credible intervals for this conditional effect did not cross zero (parameter estimate: -37.4 min; 95% credible intervals: -64.0 – -12.6 min), indicating that bats spent ca. 37 minutes less in torpor per day for each additional 1˚C in daily mean ambient temperature between 0445 hrs and 2100 hrs.

Fig. 4. Results of our simulation of daily energy expenditure by fringed myotis over the range of temperatures observed in used roosts. Each point represents one day. The red points represent estimated daily energy expenditure if bats never used torpor. The blue points represent our estimate of energy expenditure over the course of a day if part of the day is spent in torpor (with the daily duration of torpor a function of daily ambient temperature). The paler points on the left side of the graph represent simulated days below the range of temperatures we observed during the telemetry portion of our study. Estimates of daily energy expenditure incorporating observed bat behaviour are steady across roosts at temperatures above ca. 15°C, especially compared to estimates of energy expenditure if bats never used torpor. The blue points in this figure correspond with Row A in Fig. 2, and are most closely matched by Fig 2.4A. Additional simulations incorporating high and low estimates for the relationship between daily ambient temperatures and daily duration of torpor are presented in Fig. A2.

Fig. 5. Kernel density plots comparing thermal characteristics within used and available roost structures: mean temperature (A), time of day at peak temperature (B), and the standard deviation of temperature (C). Blue distributions represent used roosts, while orange distributions represent available roosts. These plots illustrate the results of our binomial model of roost selection. Used roosts were slightly warmer on average than available roosts, but their distributions largely overlapped (A). Temperatures peaked slightly earlier in used roosts than available roosts, but this was a function of temperatures in warmer roosts tending to peak earlier in the day ($r = -0.19$ for the relationship between mean temperature within roost structures and time of day at peak temperature) and their distributions largely overlap (B). The standard deviation in temperatures within used roosts is very similar to the standard deviation in temperatures within available roosts, although bats did not use the few roost structures with very high standard deviations (C). Panel A in this figure corresponds with Row B in Fig. 2, and is most closely matched by Fig. 2.4B.

Fig. 6. Scatter plot of the relationship between ambient temperature on a given day and the mean temperature within used roosts. Each point is based on observed data, and represents a roost used for one day; some roosts (n = 14) were used on multiple days and thus are represented by multiple data points on this plot. The line represents the regression line for this relationship and the grey band represents 95% confidence intervals around this line. Ambient temperature on a given day did not influence whether bats used warm or cool roosts ($p = 0.06$; $R^2 = 0.04$). This figure corresponds with Row C in Fig. 2, and is most closely matched by Fig. 2.4C.

Appendix B: Supplementary Materials

Descriptive Statistics for Rock vs. Tree Roost Structures

Temperatures within used rock crevices averaged 20.5˚C (range: 16.8˚ – 23.3˚C) while temperatures within available rock crevices averaged 19.9˚C (range: 16.5˚ – 24.2˚C). Temperatures within used tree roosts averaged 18.6˚C (range: 17.4˚ – 20.4˚C) while temperatures within available tree cavities averaged 19.2˚C (range: 16.1˚ – 25.5˚C) and temperatures within available spaces under sloughing bark averaged 18.4˚C (range: 16.1˚ – 21.0˚C).

Temperatures within used rock crevices peaked on average at 1414 hrs (range: 1105 – 1719 hrs), while temperatures within available rock crevices peaked on average at 1458 hrs (range: 1005 – 1742 hrs). Temperatures within used tree roosts peaked on average at 1447 hrs (range: 1125 – 1659 hrs), while temperatures within available tree cavities peaked on average at 1410 hrs (range: 1120 – 1608 hrs) and temperatures within available spaces under sloughing bark peaked on average at 1349 hrs (range: 1056 – 1608 hrs).

The standard deviation of temperatures within used rock crevices was 6.7˚C (range: 4.3˚ – 10.0˚C), while the standard deviation of temperatures within available rock crevices was 6.2˚C (range: 3.2˚ - 11.0˚C). The standard deviation of temperatures within used tree roosts was 7.7˚C (range: 6.7˚ - 9.1˚C), while the standard deviation of temperatures within available tree cavities was 8.7˚C (range: 5.9˚ - 16.4˚C) and within available spaces under sloughing bark was 7.7˚C (range: 6.5˚ - 11.0˚C).

There was no difference in ambient temperature between days where rock crevices were used and days where tree roost structures were used (Mann-Whitney U = 299; p = 0.968).

Table A1. Information on torpor use by bats tracked during our study, including an ID number for each individual, the dates for which we have data, the mass of bats at time of capture, the timing of torpor entry and exit for morning and afternoon bouts of torpor, the duration of periods of periods of torpor in both mornings and afternoons, and the total duration of torpor across the day.

Bat ID	Date	Mass (grams)	AM Torpor Start Time (hrs)	AM Torpor End Time (hrs)	Duration of AM Torpor (mins)	PM Torpor Start Time (hrs)	PM Torpor End Time (hrs)	Duration of PM Torpor (mins)	Total Torpor Duration (mins)
172_063	8/5/2017	6.02	517	1456	579	2013	2055	42	621
172_063	8/6/2017	6.02	451	1210	439	1910	2037	87	526
172_063	8/7/2017	6.02	2245	1557	1032	1840	2044	124	1156
172_904	6/28/2018	6.75	425	733	188	1825	2057	125	313
172_904	6/29/2018	6.75	419	1037	378	1603	2114	277	655
172_904	7/3/2018	6.75	525	944	259	1834	2029	115	374
172_904	7/4/2018	6.75	412	1446	634	1709	2122	253	887
172_904	7/5/2018	6.75	424	1458	597	1930	2043	73	670
172_904	7/6/2018	6.75	511	1016	305	-	-	0	305
172_904	7/7/2018	6.75	438	818	220	-	-	0	220
172_692	7/13/2018	6.92	445	830	225	1936	2043	67	292
172_692	7/14/2018	6.92	435	815	220	-	-	0	220
172_632	7/20/2018	8.04	426	1102	396	1916	2041	85	481
172_753	7/27/2018	8.16	133	2045	1152	-	-	0	1152
172_753	7/28/2018	8.16	2300	2031	1291	-	-	0	1291
172_453	8/4/2018	7.1	449	959	310	1915	2039	84	394
172_784	8/4/2018	7.53	442	1028	346	1951	2023	32	378
172_453	8/5/2018	7.1	459	1156	417	1613	2028	255	672

172_784	8/5/2018	7.53	445	1100	375	1852	2019	87	462
172_453	8/6/2018	7.1	441	916	275	1823	2034	131	406
172_784	8/6/2018	7.53	449	1003	314	-	-	0	314
172_453	8/7/2018	7.1	444	1041	357	-	-	0	357
172_784	8/7/2018	7.53	502	850	228	-	-	0	228
172_063	8/8/2018	6.02	2335	1427	892	1737	2009	152	1044
172_453	8/8/2018	7.1	451	839	228	-	-	0	228
172_784	8/8/2018	7.53	439	852	253	-	-	0	253
172_453	8/10/2018	7.1	456	843	227	-	-	0	227

Fig. A1. An example of raw skin temperature data that we used to delineate bouts of torpor. Periods of time in red blocks represent periods of activity (flying, foraging, etc.), periods of time in blue blocks represent periods of torpor, and periods in white represent periods of homeothermy or transition between torpor and homeothermy/activity. To delineate bouts of torpor, we used the definition suggested in Barclay, Lausen, & Hollis (2001).
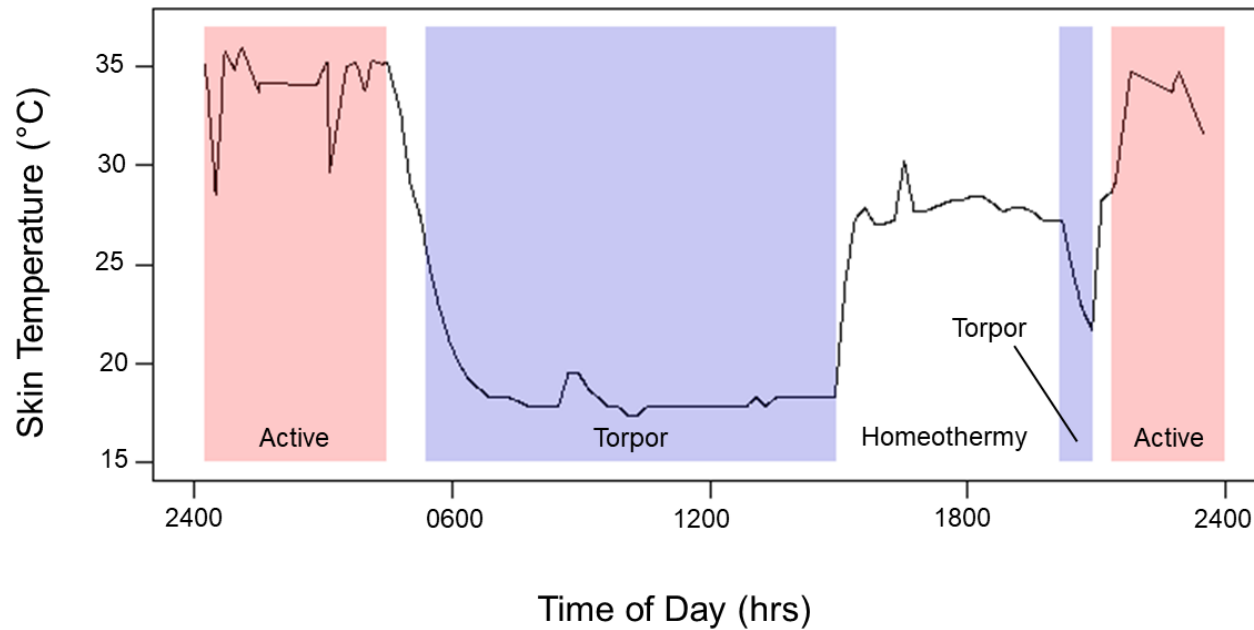
Fig. A2. Results of our simulation of daily energy expenditure by bats over the range of temperatures observed in used roosts. Each point represents one day. The red points represent estimated energy expenditure if bats maintain homeothermy all day. The blue points represent our estimate of energy expenditure over the course of a day if part of the day is spent in torpor (with the daily duration of torpor a function of daily ambient temperature). The paler points on the left side of the graph represent simulated days below the range of temperatures we observed during the telemetry portion of our study. Fig. A2.A shows that if the true relationship between daily ambient temperature and daily duration of torpor were at the upper 95% credible interval (i.e., if the slope of the relationship were substantially shallower than our mean estimate), energy expenditure would gradually increase as roosts grow colder. Fig. A2.B shows that if the true relationship between daily ambient temperature and daily duration of torpor were at the lower 95% credible interval (i.e., if the slope of the relationship were substantially steeper than our mean estimate), energy expenditure would gradually decrease until around 13°C, when it would hit a lower bound at which bats spend all day in torpor. In either of these scenarios, however, differences in energy expenditure are more gradual when bats spend some time in torpor than when bats spend all day in homeothermy.
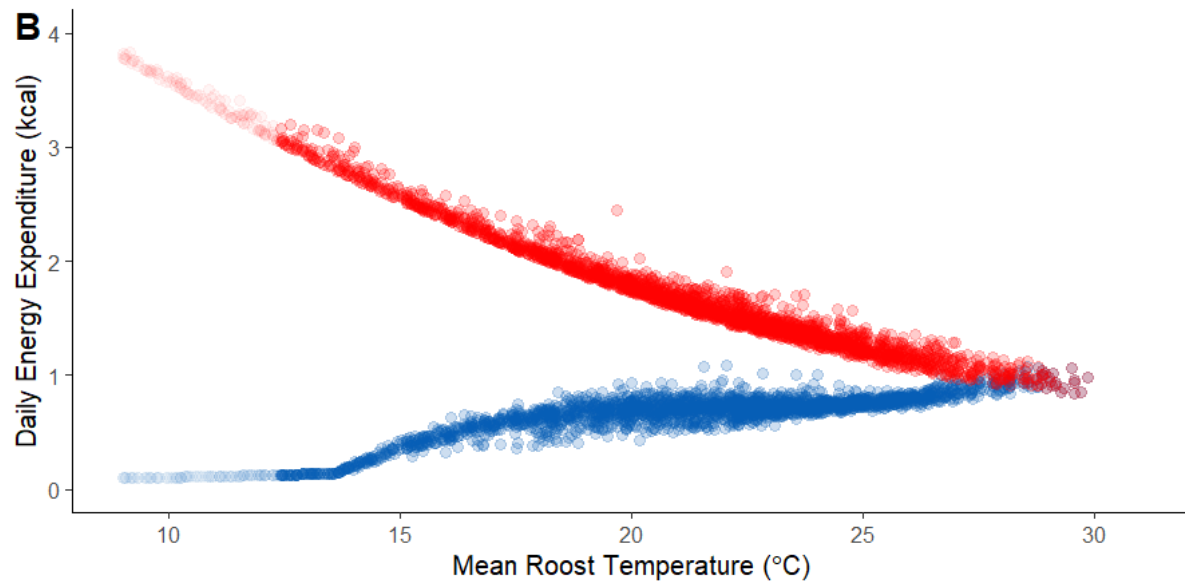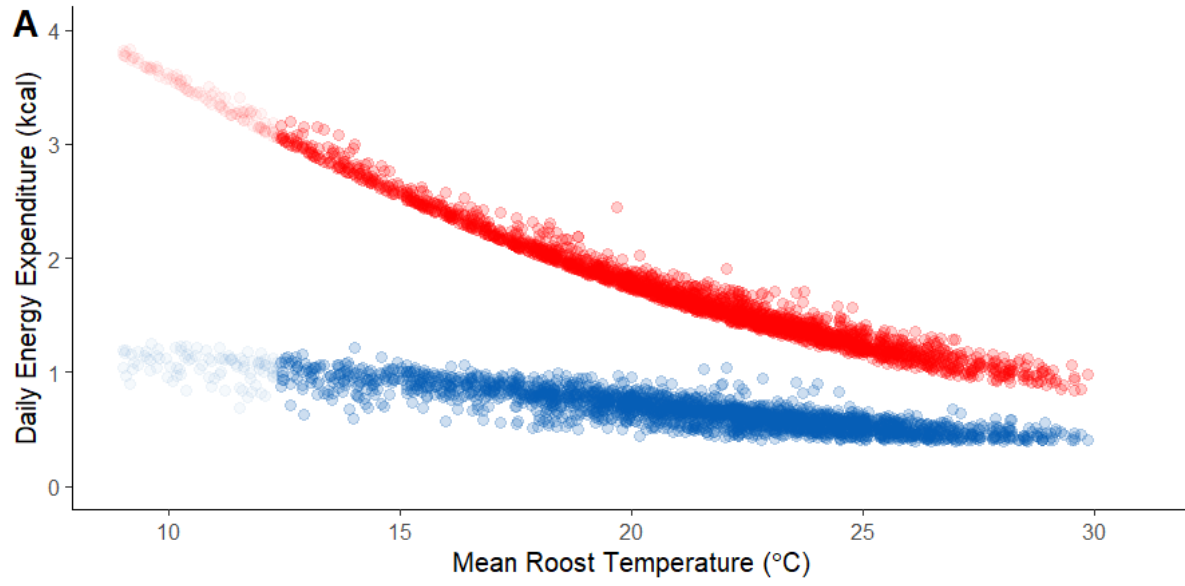
CHAPTER 3

Environmental drivers of body size in North American bats

J.M. Alston[1,2*], D.A. Keinath[3], C.K.R. Willis[4], C.L. Lausen[5], J.M. O'Keefe[6], J.D. Tyburec[7], H.G. Broders[8], P.R. Moosman[9], T.C. Carter[10], C.L. Chambers[11], E.H. Gillam[12], K. Geluso[13], T.J. Weller[14], D.W. Burles[15], and J.R. Goheen[1]

[1]Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming, USA

[2]Program in Ecology, University of Wyoming, Laramie, Wyoming, USA

[3]Wyoming Ecological Services Field Office, United States Fish and Wildlife Service, Cheyenne, Wyoming, USA

[4] Department of Biology and Centre for Forest Interdisciplinary Research, University of Winnipeg, Winnipeg, Manitoba, Canada

[5]Wildlife Conservation Society Canada, Kaslo, British Columbia, Canada

[6]Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, Urbana, Illinois, USA

[7]Bat Survey Solutions, Tucson, Arizona USA

[8]Department of Biology, University of Waterloo, Waterloo, Ontario, Canada

[9]Department of Biology, Virginia Military Institute, Lexington, Virginia, USA

[10]Department of Biology, Ball State University, Muncie, Indiana USA

[11]School of Forestry, Northern Arizona University, Flagstaff, Arizona, USA

[12]Department of Biological Sciences, North Dakota State University, Fargo, North Dakota, USA

[13]Department of Biology, University of Nebraska at Kearney, Kearney, Nebraska, USA

[14]Pacific Southwest Research Station, United States Forest Service, United States Department of Agriculture, Arcata, California, USA

[15]Parks Canada, Gwaii Haanas National Park Reserve and Haida Heritage Site, Queen Charlotte, British Columbia, Canada

*Corresponding author: jalston@uwyo.edu

Abstract

Bergmann's Rule—which posits that larger animals live in colder areas—is thought to influence variation in body size within species across space and time, but evidence for this claim is mixed. We tested four competing hypotheses for spatio-temporal variation in body size within bat species during the past two decades across North America. Bayesian hierarchical models revealed that spatial variation in body mass was most strongly correlated with mean annual temperature, supporting the heat conservation hypothesis (the mechanism historically believed to underlie Bergmann's Rule). Across time, variation in body mass was most strongly correlated with net primary productivity, supporting the resource availability hypothesis. Climate change may influence body size in animals but will likely do so through both changes in mean annual temperature and in resource availability. Rapid reductions in body size alongside climate change have occurred in short-lived, fecund species, but such reductions may transpire more slowly in longer-lived species.

Key words   Bayesian hierarchical modeling, Bergmann's Rule, body size clines, Chiroptera, climate change, geographic information systems, primary productivity

Introduction

Body size influences every aspect of organismal biology, including lifespan (Lindstedt & Calder 1981; Speakman 2005), metabolism (Brown *et al.* 2004; Clarke *et al.* 2010), movement rates (Jetz *et al.* 2004; Noonan *et al.* 2020), reproductive biology (Fenchel 1974; Blueweiss *et al.* 1978), and extinction risk (Brown 1995; Ripple *et al.* 2017). Understanding the factors that drive variation in body size is thus among the most important goals in ecology (Kaspari 2005).

Bergmann's Rule (Bergmann 1847; Salewski & Watt 2017), which states that animals residing in colder climates are larger than those residing in warmer climates, is a widely known macroecological pattern. Although originally and primarily applied to differences in body size between closely related species, Bergmann's Rule is often believed to extend to within-species differences in body size as well (Ashton 2002; Meiri & Dayan 2003; Blackburn & Hawkins 2004; Watt *et al.* 2010; Riemer *et al.* 2018).

The mechanism traditionally hypothesized to underlie Bergmann's Rule is an increased ability to conserve body heat with increasing body size (hereafter, the "heat conservation hypothesis"; (Bergmann 1847; Mayr 1956; Ashton 2002; Watt *et al.* 2010). To maintain a stable, elevated body temperature, endotherms must operate at higher metabolic rates when faced with cooler ambient temperatures, and thus experience substantial loss of metabolic heat to the environment (McCafferty *et al.* 2011; Fristoe *et al.* 2015). Because the ratio between surface area and volume decreases with increasing body size, heat loss relative to mass decreases faster than metabolic rate relative to mass, although absolute heat loss increases with increasing body size (Withers *et al.* 2016). Larger body size may thus be an adaptation to climates with cooler average temperatures.

Despite its intuitive appeal, empirical evidence supporting the heat conservation hypothesis within species is mixed. Although ecologists have accumulated substantial evidence that individuals within species tend to be larger in colder climates (e.g., (Smith *et al.* 1995; Ashton 2002; Meiri & Dayan 2003), more recent and more comprehensive tests have failed to find consistent relationships between temperature and the body sizes of individuals within species (Riemer *et al.* 2018). Additionally, physiologists have questioned the validity of the heat conservation hypothesis on physiological grounds (Scholander 1955; McNab 1971; Geist 1987).

In sum, and despite the widespread acceptance of the heat conservation hypothesis in the ecological literature, the extent to which variation in temperature translates to variation in body size within species remains an open question.

Because of skepticism surrounding the primary mechanism by which Bergmann's Rule is assumed to occur, ecologists have proposed other hypotheses to explain geographical clines in body size within species that are consistent with Bergmann's Rule (Meiri *et al.* 2007; Salewski & Watt 2017). For example, larger individuals have lower critical thermal maxima, and thus experience greater risk of mortality than smaller individuals at high temperatures (hereafter the 'critical thermal maximum hypothesis'). This idea posits an additional (or alternative) mechanism by which animals from colder climates are larger than their counterparts from warmer climates, and is supported in the genus *Neotoma* (i.e., woodrats; (Brown & Lee 1969; Smith *et al.* 1995). A second alternative is the 'resource availability hypothesis', through which increased resource availability results in larger individuals, so that resource availability—which often is correlated with temperature across the globe (Gillman *et al.* 2015; Chu *et al.* 2016)—drives biogeographical patterns in body size (e.g., (Rosenzweig 1968; McNab 2010; Huston & Wolverton 2011; Yom-Tov & Geffen 2011; Kelly *et al.* 2018). If true, clinal variation in body size consistent with Bergmann's Rule could arise over limited geographic areas (e.g., an elevational gradient where increased precipitation increases productivity even as temperature decreases), although body sizes should *decrease* as temperatures decrease (contra Bergmann's Rule) at very large (i.e., continental) spatial scales. Finally, a third hypothesis proposed to explain Bergmann's Rule is the 'starvation resistance' (or 'seasonality') hypothesis. According to this hypothesis, large body size buffers against resource scarcity driven by seasonality (Boyce 1979). Because seasonality increases at higher latitudes and fasting endurance decreases with decreasing temperature (Lindstedt & Boyce

1985), this dynamic may produce a size cline consistent with Bergmann's Rule. The starvation resistance hypothesis has received support from studies on songbirds (Jones *et al.* 2005), muskrats (*Ondatra zibethicus*; (Boyce 1978), and bobcats (*Lynx rufus*; (Wigginton & Dobson 1999).

Many ecologists and evolutionary biologists have extended Bergmann's Rule to apply over time (e.g., (Smith *et al.* 1995; Van Buskirk *et al.* 2010; Merckx *et al.* 2018; Weeks *et al.* 2020). In other words, as temperatures fluctuate over time, the average size of individuals within a species is expected to decrease as temperatures rise, and to increase as temperatures fall. Although early studies of this temporal equivalent to Bergmann's Rule focused on time scales of thousands of years (Smith *et al.* 1995), more recent studies have found that changes in body size can occur over decades or even years (e.g., (Van Buskirk *et al.* 2010; Weeks *et al.* 2020). However, and similar to the original (spatial) conceptualization of Bergmann's Rule, empirical evidence for this temporal equivalent is mixed (Sheridan & Bickford 2011; Yom-Tov & Geffen 2011; Teplitsky & Millien 2014), perhaps because other mechanisms—analogous to alternative mechanisms for Bergmann's Rule detailed in the paragraph above—influence shifts in body size over time. Evidence suggests that alternative mechanisms underlying Bergmann's Rule are plausible as temporal drivers of body size if they influence body size over space. Extreme climatic events can trigger rapid evolution of traits (Campbell-Staton *et al.* 2017; Donihue *et al.* 2018), which is consistent with the critical thermal maximum and starvation resistance hypotheses. The large literature documenting positive effects of resource availability on fat reserves and growth (e.g., (Brett 1971; Boutin & Larsen 1993; Altmann & Alberts 2005; Monteith *et al.* 2014) would support the resource availability hypothesis. Testing these alternative hypotheses across both space and time provides a lens through which to anticipate how changes in climate may affect body size in the future, as well as the pace at which any changes in body size may occur.

To evaluate the mechanistic underpinnings of Bergman's Rule, we tested whether spatial and temporal variation in body mass of North American bats is best supported by the heat conservation, critical thermal maximum, resource availability, or starvation resistance hypotheses (summarized in Table 1). We used Bayesian hierarchical models to weigh evidence for each hypothesis across both space and time for 20 species of North American bats. We expected observed patterns of variation in body mass to be driven by the same process or processes across both time and space. In other words, if variation in body mass across space were best explained by one of our four hypotheses, we also expected variation in body mass across time to be best explained by the same hypothesis, which would provide strong evidence for a consistent selective force driving variation in body size.

Methods

2.1 Data Collection

We compiled biometric data on bats captured throughout North America (Fig. 1). All biometric data contained information on capture location, date of capture, species, sex, age class, reproductive state, and mass. Because body mass varies with species, sex, age class, reproductive state, and time of year, we accounted for potential variation due to these differences by calculating the mean mass for each species/sex/reproductive state combination in each month, subtracting the equivalent mean value from the mass of each individual in the data set, and dividing this by the standard deviation of body mass values for that species. We only included data from adult bats captured between April and October in the final data set used for analysis. We also excluded species that were represented by < 150 individuals or occurred across < 2.5° of latitude.

To test hypotheses for clinal variation in body mass, we extracted environmental variables from remotely sensed raster data sets. To test the heat conservation hypothesis across space, we extracted data for each capture location from the 30-second (~1 km) resolution version of the WorldClim 2.1 mean temperature data set (mean annual temperature, 1970-2000; (Fick & Hijmans 2017). We centered mean annual temperatures in our data set at zero by subtracting the mean annual temperature across all capture locations. To test the heat conservation hypothesis across time, we extracted data for each capture location from the DAYMET daily climate summaries 1-km resolution data set (Thornton *et al.* 2020) using the 'daymetr' package (version 1.4; (Hufkens *et al.* 2018). We used that data to calculate the midpoint of low and high temperatures across all days from 1 April until the date each bat was captured, and then subtracted the average of this value at the capture location during our study period (2000-2016) to obtain a final centered metric of year-to-year differences in mean temperatures. This represents roughly the period in which a bat would be active in a given year (dates before 1 April are likely to be spent in hibernation or in winter ranges).

To test the critical thermal maximum hypothesis across space, we extracted data for each capture location from the DAYMET daily climate summaries 1-km resolution data set (Thornton et al. 2020) and used that data to calculate the maximum temperature at each capture location in each year between 1980 and 2010 (the earliest 30-year period available). We then calculated the mean annual maximum temperature across this 30-year period at each site and subtracted the mean annual maximum temperature across all sites to obtain a final centered metric of long-term maximum annual temperatures. To test the critical thermal maximum hypothesis across time, we extracted data for each capture location from the DAYMET daily climate summaries 1-km resolution data set (Thornton et al. 2020). We calculated the maximum temperature in the prior

365 days for each bat capture event, then subtracted the long-term average for this value at the site of capture to calculate a final centered metric of year-to-year differences in maximum temperatures.

To test the resource availability hypothesis across space, we extracted data for each capture location from the 0.1-degree (~10 km) resolution version of the MODIS monthly net primary productivity data set (Stockli 2020). Primary productivity is positively correlated with insect biomass across both space (Borer *et al.* 2012; Lind *et al.* 2017) and time (Bell 1985; Frith & Frith 1985). We averaged monthly net primary productivity across months during the active season for bats (April-October) for all available years (2000-2016), then divided by the mean value across all sites to obtain a final metric centered at one. To test the resource availability hypothesis across time, we extracted data from the same rasters and averaged net primary productivity for months preceding the date a bat was captured (in the year of capture, inclusive of the month of capture, starting in April), then divided by the average of this value at the site of capture for the entire time period.

To test the starvation resistance hypothesis across space, we extracted data for each capture location from the 30-second (~1 km) resolution version of the WorldClim 2.1 minimum temperature data set (mean minimum temperature, 1970-2000; Fick and Hijmans 2017). To estimate the severity of resource limitation in the period in which bats are most resource-limited, we averaged minimum temperatures across the months of September, October, April, and May, which roughly represent night-time temperatures during the time period where bats tend to be most energetically vulnerable. Regardless of whether they hibernate or migrate for the winter, bats at temperate latitudes must gain a substantial amount of weight in the fall (Kunz *et al.* 1998; Lacki *et al.* 2015; Guglielmo 2018; Cheng *et al.* 2019; Sommers *et al.* 2019), and they tend to be

energetically stressed in the early spring before insects become abundant (Arlettaz *et al.* 2001; Encarnação *et al.* 2004; Jonasson & Guglielmo 2019). Low temperatures during fall and spring thus represent a reasonable proxy for winter severity. We centered mean minimum spring and fall temperatures in our data set at zero by subtracting the mean minimum spring and fall temperature across all capture locations.   To test the starvation resistance hypothesis across time, we extracted data from the DAYMET daily climate summaries 1-km resolution data set (Thornton et al. 2020). We averaged the minimum daily temperatures for the spring (April and May) and fall (September and October) preceding the date on which a bat was caught, and subtracted the average value at the site of capture during our study period.

2.2 Statistical Analysis

We used the R statistical software environment (version 4.0.2; (R Core Team 2020) to quantify the influence of our environmental variables on bat body mass across both space and time. We used the modelling software 'Stan' (Carpenter *et al.* 2017) via the R package 'brms' (version 2.13.3; (Bürkner 2017) to build a single Gaussian-family Bayesian model for each species to quantify the effects on body mass of the environmental predictors detailed above. Each model included 3 chains that were run for 12,000 iterations (2,000 iterations of warm-up and 10,000 iterations of sampling). We assessed chain convergence using the Gelman-Rubin diagnostic ($\hat{R}$) and precision of parameter estimation using effective sample size. $\hat{R} < 1.01$ and effective sample sizes $> 10,000$ represent acceptable convergence and parameter precision (Gelman *et al.* 2013; Kruschke 2015). We used leave-one-out cross-validation to check model fit using the R packages 'loo' (version 2.3.1; (Vehtari *et al.* 2017) and 'bayesplot' (version 1.7.2; (Gabry *et al.* 2019) to visually assess the cross-validated probability integral transform.

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Results

The final data set contained 31,303 individuals of 20 species captured at 1,190 locations (Fig. 1; Table A1). Significant spatial and temporal variation existed among all predictor variables, enabling detection of meaningful relationships between body mass and predictor variables (Fig. A1; Fig. A2).

Spatial Variation in Body Mass

Spatial variation in body mass most strongly supported the heat conservation hypothesis, with most species exhibiting greater body mass in areas with colder mean annual temperatures (Fig. 2A). For 15 out of 20 species, body mass declined with increasing mean annual temperature (i.e., $\beta < 0$), and the probability that the slope was below zero was >95% for 6 of these species. Most species exhibited minimal variation in body mass with respect to maximum temperature (Fig. 2B), primary productivity (Fig. 2C), and spring and fall temperatures (Fig. 2D), suggesting a lack of support for the critical thermal limits, resource availability, and starvation resistance hypotheses, respectively. For these three hypotheses, slopes were relatively evenly distributed around 0; 90% credible intervals overlapped with 0 in most cases, and credible intervals that did not overlap zero were distributed relatively evenly around zero.

Temporal (Interannual) Variation in Body Mass

Temporal variation in body mass most strongly supported the resource availability hypothesis, with most species, with most species exhibiting greater body mass during years in which net primary productivity was higher (Fig. 3C). For 14 out of 20 species, body mass declined with

increasing net primary productivity (i.e., β > 0), and the probability that the slope was above zero was >95% for 7 of these species. Most species exhibited little variation in body mass with respect to year-to-year differences in mean annual temperatures (Fig. 3A), maximum temperatures (Fig. 3B), or spring/fall temperatures (Fig. 3D), suggesting a lack of support for the heat conservation, critical thermal limits, and starvation resistance hypotheses, respectively For these tests, slopes were relatively evenly distributed around 0, 90% credible intervals overlap with 0 in most cases, and credible intervals that do not overlap zero are relatively evenly distributed around zero or are distributed in the direction opposite the majority of most coefficients.

Discussion

Although intraspecific clines in body size have received attention for nearly two centuries (Bergmann 1847; Watt *et al.* 2010), recent studies have cast doubt on both their prevalence and the generality of the mechanisms underlying them (e.g., (Meiri *et al.* 2007; Muñoz *et al.* 2014; Freeman 2017; Riemer *et al.* 2018). We used North American bats as a model system to test four competing hypotheses (Table 1) for intraspecific variation in body mass consistent with Bergmann's Rule, a well-known macroecological pattern. Further, because recent evidence suggests that the mechanisms underlying such geographical clines may be causing rapid evolutionary change in body size (e.g., Van Buskirk et al. 2010; Merckx et al. 2018; Weeks et al. 2020), we also tested the ability of these four hypotheses to describe interannual variation in body mass. Although no hypothesis perfectly described variation in body mass across every species, spatial variation in body mass of bats was most consistently correlated with mean annual temperature (supporting the heat conservation hypothesis), and temporal variation in body mass was most consistently correlated with net primary productivity (supporting the resource

availability hypothesis). In tandem, our results highlight that both spatial and temporal patterns of variation in body size have an energetic basis, but via two distinct pathways: spatial variation in body size is driven by energy loss to the environment in the form of heat, and temporal variation in body size is driven by energy gain from abundant food.

Across North America, body mass of bats was most strongly correlated with mean annual temperature, matching the traditional hypothesis—the heat conservation hypothesis—for Bergmann's Rule. However, this mechanism had little influence on temporal variation in body size, perhaps because selective pressure via size-dependent differences in energy expenditure may take considerable time to manifest. Compared to the critical thermal limits and starvation resistance hypotheses—which assume the occurrence of acute mortality events driven by extreme heat and severe resource scarcity, respectively—the heat conservation hypothesis posits more gradual selection on body size. Differences in survival and reproduction between small individuals and large individuals may therefore fail to manifest in measurable population-level variation in body size, even after unusually warm or cold years. Only after climate departs from historical norms over many generations should body size change at the population level.

Recent research has questioned the assumption that the heat conservation hypothesis underlies Bergmann's Rule (Riemer et al. 2018). Using museum specimens of a wide array of endotherms (including bats) collected across the globe, Riemer et al. (2018) found that intraspecific variation in body mass did not vary with mean annual temperature. Our results contradict this finding, likely because we were able to control for sources of variation in body mass (e.g., sex, reproductive status, time of year, resource availability) that may confound simpler analyses. A diverse host of factors contributes to variation in body mass, and their cumulative influence could swamp variation driven by mean annual temperature. Given this challenge,

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compiling very large samples and carefully accounting for potential confounds is necessary for clarifying the extent to which mean annual temperature drives variation in body size within species.

That resource availability might drive body mass variation temporally but not spatially follows predictions of the "ideal free distribution" model of resource selection (Fretwell & Lucas 1969; Royama 1970) and the "more-individual hypothesis" for species-energy relationships (Wright 1983; Srivastava & Lawton 1998; Storch *et al.* 2018). If individuals within a species are distributed in an ideal free manner, populations should be denser in areas with greater resource availability, such that *per capita* resource availability is roughly equivalent over their geographic range. In this scenario, individuals should not be appreciably larger or heavier in resource-rich areas than in resource-poor areas, but populations should be denser or sparser, respectively. In other words, additional energy is converted into additional individuals (rather than larger individuals). However, if resource availability changes from year to year, this equilibrium can be disrupted, leading to temporary situations in which *per capita* resource availability is higher in some areas than others until population densities reach a steady state of resource availability. In this scenario, individuals are likely to be larger or heavier in (temporarily) resource-rich areas than in (temporarily) resource-poor areas, and this temporal variation in body mass is driven more by changes in nutritional condition (i.e., fat reserves and muscle mass) than by differences in body size arising from directional selection. This dynamic is likely to be particularly pronounced in bats and other long-lived species that produce few offspring, because population density cannot rapidly track changes in resource availability via increases in recruitment.

Importantly, our analysis shows that the processes that drive spatial patterns in body size are unlikely to result in equivalent temporal patterns, at least over ecological time scales. Variation

in body size occurs both temporally and spatially, but the underlying processes are likely distinct and may manifest over markedly different timescales. Motivated by patterns of spatial variation in body size, many investigators have attempted to quantify analogous patterns through time, typically over the course of years or decades (Sheridan & Bickford 2011; Caruso *et al.* 2014; Teplitsky & Millien 2014). However, spatial patterns may take centuries or millennia to arise, even when they are relatively clear-cut (and spatial patterns in body size are rarely so). This is especially true for long-lived species, for which the pace of change is likely to be slower than for short-lived, more fecund species.

Climate change will likely induce changes in body size for animals, but such changes may be more complex than has been appreciated. Over the nearly 2 decades that we collected data, the primary driver of short-term (annual) variation in body size was resource availability. Increases in mean annual temperatures will make many ecosystems more productive for a longer portion of the year, and changes in precipitation will either accentuate or dampen such shifts in productivity (Chu *et al.* 2016; La Pierre *et al.* 2016). Any changes in body size driven by climate change will therefore depend on the extent to which mean annual temperature, the amount of precipitation, and the timing of precipitation are altered for a given area. Moreover, and because net primary productivity does not meaningfully influence body size across space, any such changes may be transient, renormalizing over time if humans eventually curb greenhouse gas emissions.

Life history traits should mediate the influence of climate change on body size. The most compelling evidence of rapid changes in body size due to climate change comes from songbirds (e.g., Van Buskirk et al. 2010, Weeks et al. 2020), which are shorter lived and more fecund than bats. Because pace of life is positively correlated with the pace of evolution (i.e., smaller, more fecund species tend to evolve more rapidly; (Martin & Palumbi 1993; Gillooly *et al.* 2005; Nabholz

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et al. 2008), the processes that lead to spatial variation in body size should arise faster over time in short-lived species than long-lived species. To accurately quantify the extent and pace of reductions in body size due to climate change, further studies are needed to enable direct comparisons of the pace of body size change across taxa with different life histories.

While recent evidence indicates that climate change is inducing rapid evolution in body size in some species (Van Buskirk *et al.* 2010; Gardner *et al.* 2011; Weeks *et al.* 2020), we found no evidence that this is occurring in bats. Spatial variation in body mass of North American bats is consistent with the heat conservation hypothesis for Bergmann's Rule, but the heat conservation hypothesis does not explain variation in body size over time. Instead, temporal variation in body mass over the past two decades appears to be driven largely by resource availability. For bats and other long-lived species, temperature-induced reductions in body size may take substantially longer to manifest than for short-lived, more fecund species, and will be obscured by variation in resource availability.

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Figures and Tables

Table 1. Descriptions of the hypotheses tested in this paper, including the name, spatial version of the hypothesis, proxy data used to

test the spatial hypothesis, temporal version of the hypothesis, and proxy data used to test the temporal hypothesis.

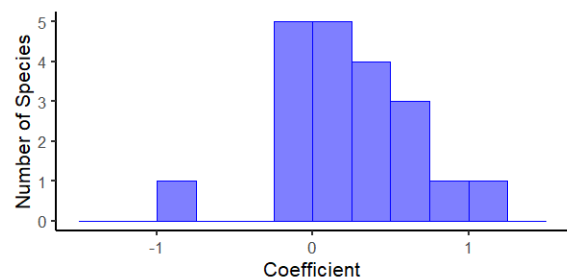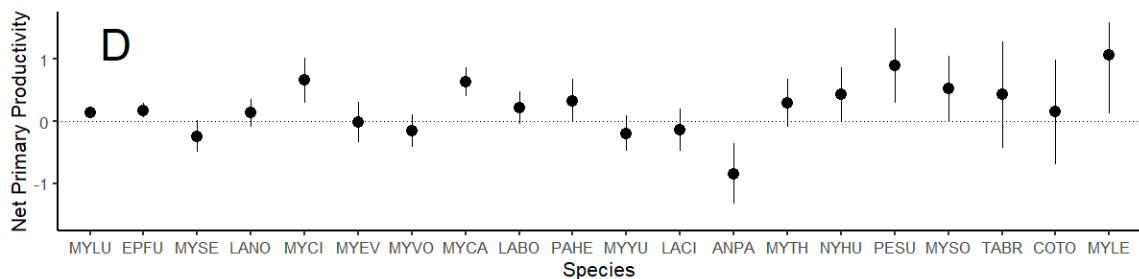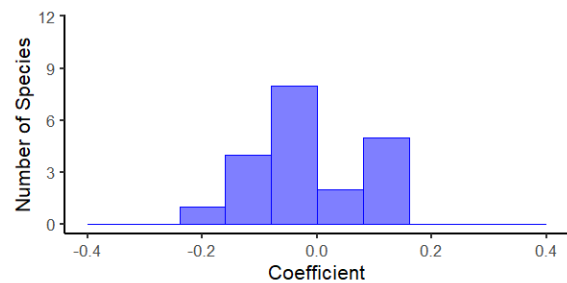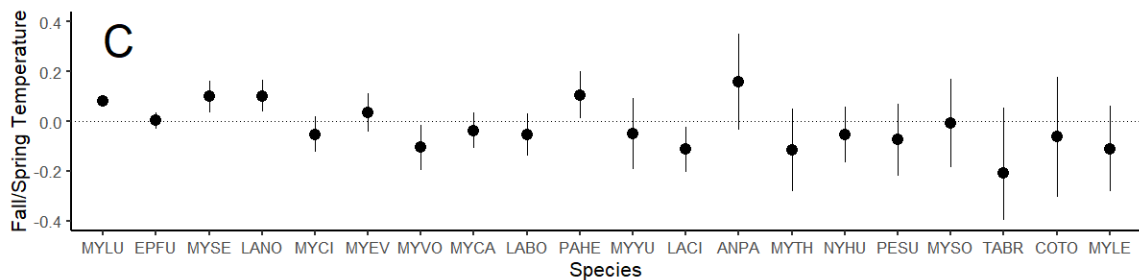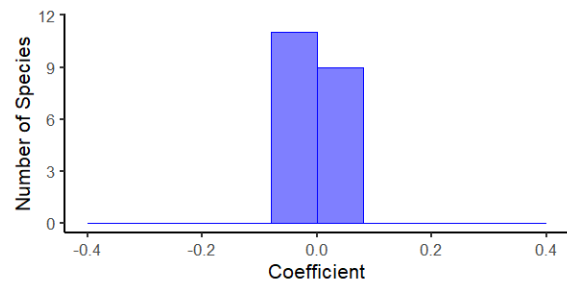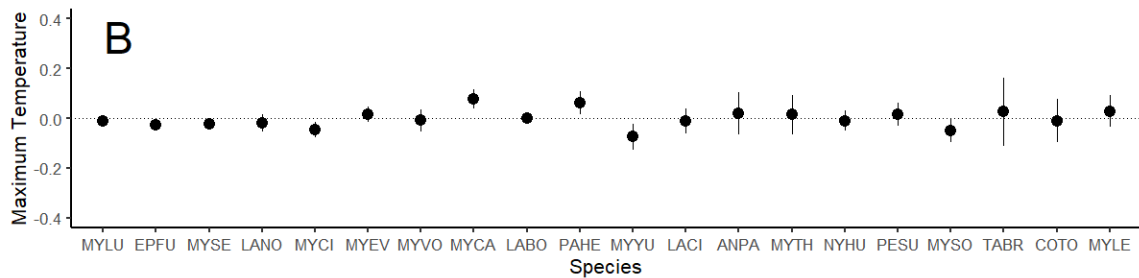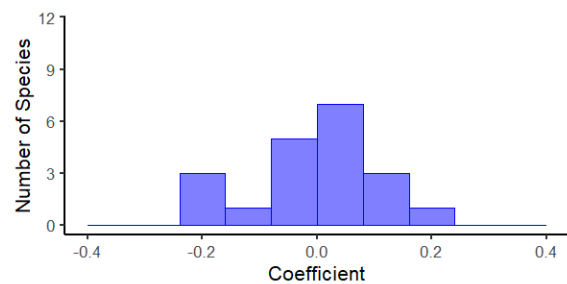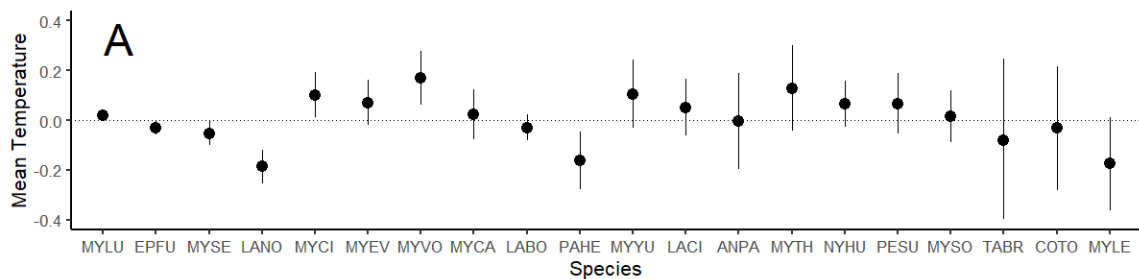| Hypothesis Name	Spatial Hypothesis	Spatial Proxy Data	Temporal Hypothesis	Temporal Proxy Data
Heat Conservation	Because larger body size increases an individual's ability to conserve body heat, individuals will be larger in areas where average temperatures are lower.	Mean annual temperature (1970-2000; WorldClim; Fick and Hijmans 2017)	Because larger body size increases an individual's ability to conserve body heat, individuals will be larger in years in which average temperatures are lower.	Mean temperature from April 1 of capture year until date of capture (DAYMET; Thornton et al. 2020)
Critical Thermal Maximum	Because larger individuals tend to have lower critical thermal maxima, individuals will be smaller in areas where maximum temperatures are lower.	Mean annual maximum temperature (1980-2010; DAYMET; Thornton et al. 2020)	Because larger individuals tend to have lower critical thermal maxima, individuals will be smaller in years in which maximum temperatures are lower.	Maximum temperature in the preceding 365 days (DAYMET; Thornton et al. 2020)
Resource Availability	Because individuals living in more productive environments tend to be larger, individuals will be larger in areas where primary productivity is higher.	Net primary productivity during April – October (2000-2016; MODIS; Stockli 2020)	Because individuals living in more productive environments tend to be larger, individuals will be larger in years in which primary productivity is higher.	Net primary productivity in months preceding capture, inclusive of month of capture (MODIS; Stockli 2020)
Starvation Resistance	Because larger body size increases an individual's ability to survive periods of resource scarcity, individuals will be larger in areas where periods of resource scarcity (e.g., winters) are most severe.	Average minimum temperature in April, May, September, and October (1970-2000; WorldClim; Fick and Hijmans 2017)	Because larger body size increases an individual's ability to survive periods of resource scarcity, individuals will be larger in years in which periods of resource scarcity (e.g., winters) are most severe.	Average minimum temperature in the April, May, September, and October preceding capture (DAYMET; Thornton et al. 2020)

Fig. 1. Map of capture locations for bats included in our analyses. Our final data set included 31,303 bats sampled from 1,190 sites along a >30° gradient in latitude.

Fig. 2. Intraspecific patterns in body mass across space in 20 species of North American bats, which most strongly support the heat conservation hypothesis. In the left column, we plotted the slope for each species' relationship between body mass and the predictor variable of interest (points) and 90% credible intervals (lines). Points above the dotted line at 0 indicate species in which individual body mass increased as the variable of interest increased. Species are ordered from largest (left) to smallest (right) sample sizes. In the right column, we plotted histograms of the coefficients. Row A represents the heat conservation hypothesis, Row B represents the critical thermal limits hypothesis, Row C represents the starvation resistance hypothesis, and Row D represents the resource availability hypothesis. Distributions centered on zero indicate no consistent effect of the variable of interest on body mass, while distributions centered asymmetrically around zero indicate directional effects. Credible intervals were truncated at the limit of the y-axis for ease of interpretability. The mean estimate of the coefficient for the effect of net primary productivity on body mass for *Myotis leibii* (4.29) was excluded from the y-axis of that graph to ease interpretability, but the 90% credible interval for that estimate crosses zero as shown in the graph. Species codes are listed in Table A1.

Fig. 3. Intraspecific patterns in body mass across time in 20 species of North American bats, which most strongly support the resource availability hypothesis. In the left column, we plotted the slope for each species' relationship between body mass and the predictor variable of interest (points) and 90% credible intervals (lines). Points above the dotted line at 0 indicate species with larger masses as the variable of interest increased. Species are ordered from largest (left) to smallest (right) sample sizes. In the right column, we plotted histograms of the coefficients. Row A represents the heat conservation hypothesis, Row B represents the critical thermal limits hypothesis, Row C represents the starvation resistance hypothesis, and Row D represents the resource availability hypothesis. Distributions centered on zero indicate no consistent effect of the variable of interest on body mass, while distributions centered asymmetrically around zero indicate consistent effects. Credible intervals were truncated at the limit of the y-axis for ease of interpretability. Species codes are listed in Table A1.

Appendix C: Supplementary Materials

Table A1. Table including species included in our analysis, species code (used in figures), the number of individuals included in each

species' model, the latitudinal range covered by individuals of each species (in degrees), and the number of distinct site-year

combinations at which each species was captured.

Species	Species Code	Number of Individuals	Latitudinal Range	Number of Site-years
Antrozous pallidus	ANPA	567	17.50	136
Corynorhinus townsendii	COTO	234	18.32	92
Eptesicus fuscus	EPFU	4,123	28.29	551
Lasiurus borealis	LABO	918	18.55	132
Lasiurus cinereus	LACI	824	20.82	236
Lasionycteris noctivagans	LANO	1,572	20.73	300
Myotis californicus	MYCA	1,183	21.98	212
Myotis ciliolabrum	MYCI	1,540	20.07	318
Myotis evotis	MYEV	1,353	21.17	384
Myotis leibii	MYLE	150	8.11	67
Myotis lucifugus	MYLU	12,293	23.53	693
Myotis septentrionalis	MYSE	1,702	25.39	243
Myotis sodalis	MYSO	285	2.54	48
Myotis thysanodes	MYTH	495	18.90	159
Myotis volans	MYVO	1,309	24.38	307
Myotis yumanensis	MYYU	847	18.24	136
Nycticeius humeralis	NYHU	403	13.59	59
Parastrellus hesperus	PAHE	905	8.73	129
Perimyotis subflavans	PESU	339	14.50	86
Tadarida brasiliensis	TABR	261	10.50	59

Fig. A1. Intraspecific patterns in body mass across latitude and year in 20 species of North American bats. In the left column, we plotted each species' regression coefficient (points) and 90% credible interval (lines). Points above the dotted line at 0 indicate species with larger masses as the variable of interest increased. Species are ordered from largest (right) to smallest (left) sample sizes. In the right column, we plotted histograms of the coefficients. Distributions centered on zero indicate no consistent effect of a predictor on body mass, while distributions centered asymmetrically around zero indicate consistent effects.
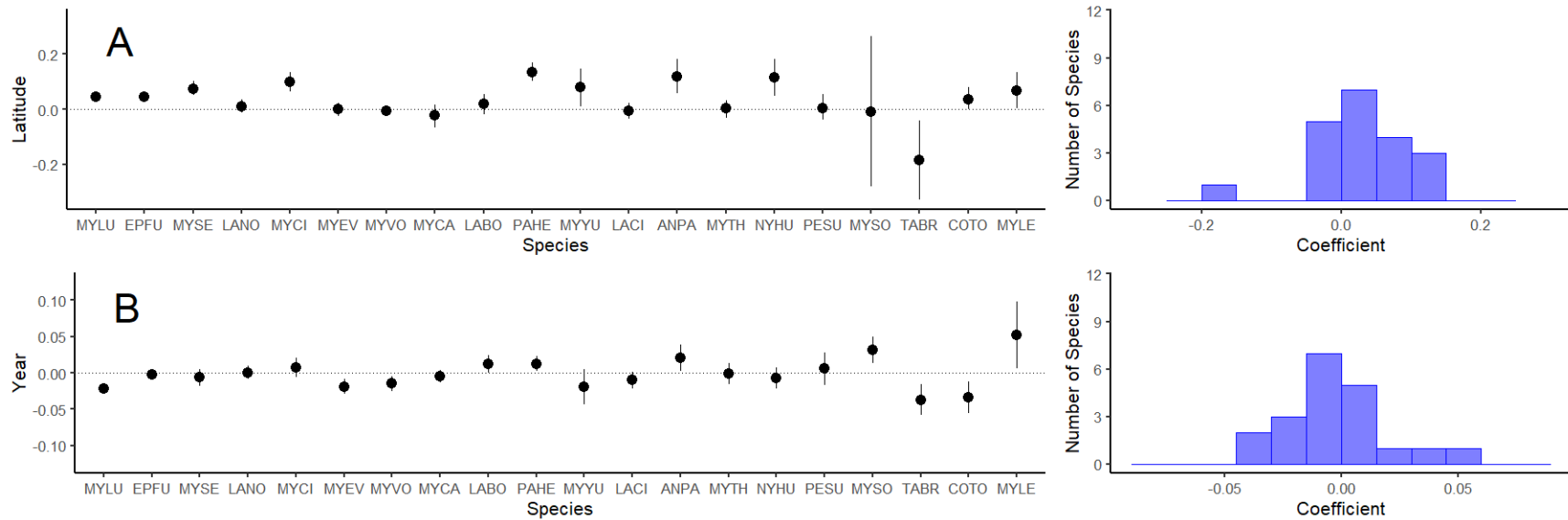
Fig. A2. Scatterplots depicting relationships between latitude and variables of interest (left column), and year and variables of interest (right column). Each point represents one capture location, trend lines represent a linear regression of the trend across space or time, and the color of the points represents the number of bats captured at a location (darker points denote more captures). Confidence intervals (95%) are represented by gray ribbons (which are very narrow in all regressions due to large sample sizes). Contrary to expectations, net primary productivity at capture sites increased at higher latitudes (due in part to a large number of bats captured in the arid southwestern United States where primary productivity is low, and the exclusion of winter months when primary productivity is much lower at more northern sites). Following expectations, mean annual temperatures, maximum temperatures, and spring and fall temperatures decreased as latitude increased. If body size is driven by any of these predictor variables, geographic variation in each of these predictor variables (or some combination thereof) could create a spatial pattern of body mass consistent with Bergmann's Rule. Across time during our study period, spring and fall temperatures and net primary productivity increased, while mean annual temperatures and maximum temperatures were relatively constant. Consequently, only spring and fall temperatures and net primary productivity could lead to an observed trend of shrinking body mass over time during our study. Nevertheless, interannual variation in each of these variables was substantial, so if any of these predictor variables are initiating rapid evolutionary change in body size, our analyses are likely to detect it.
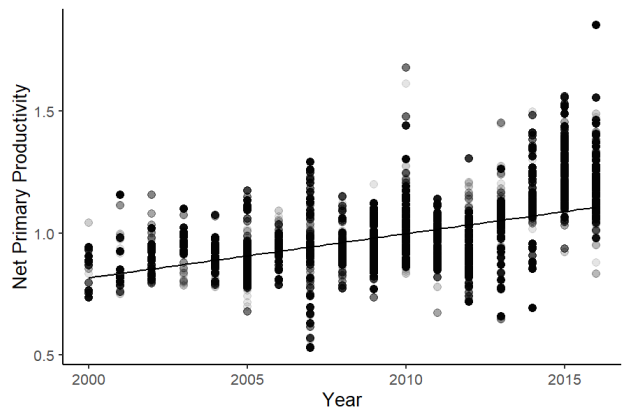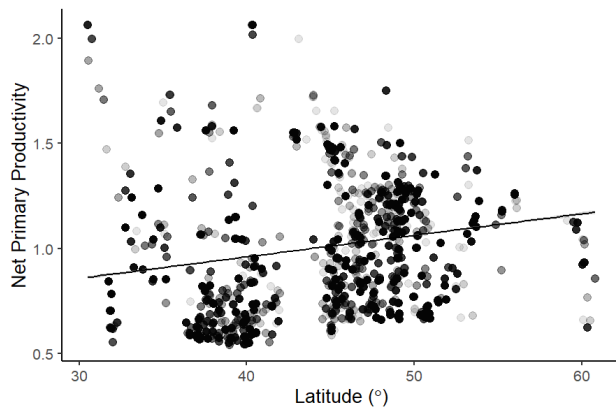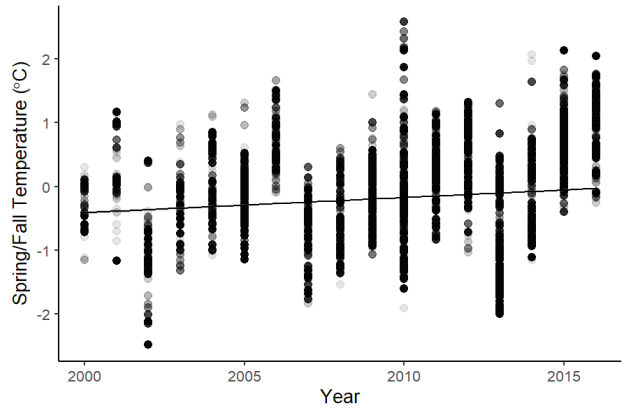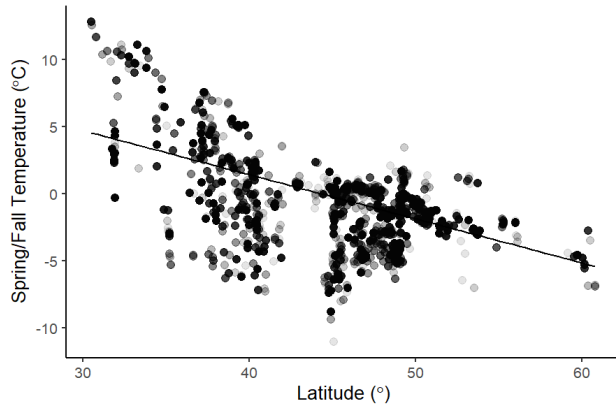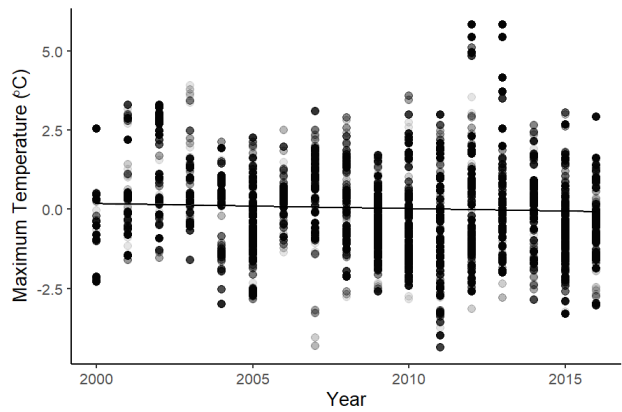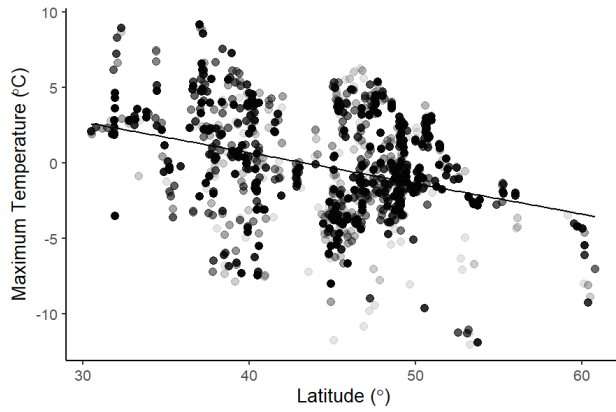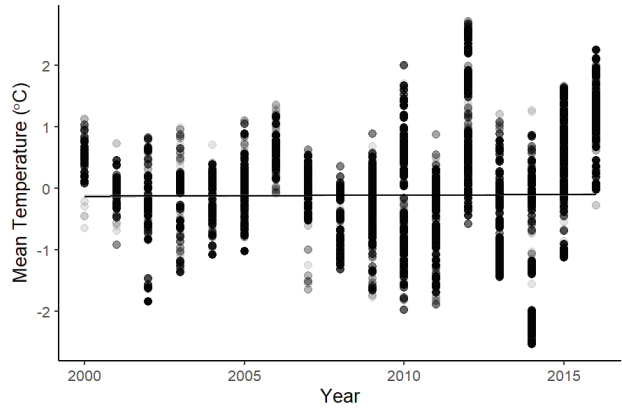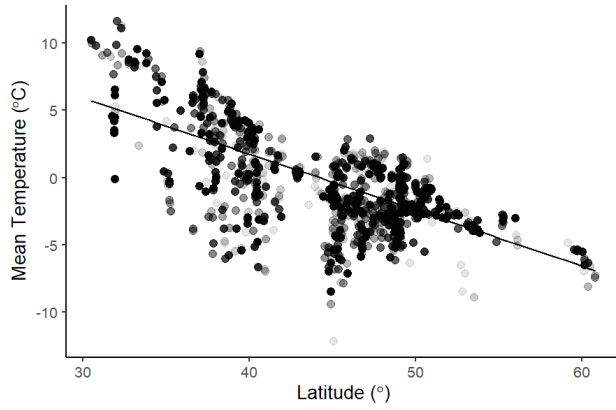
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