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Metabolic rate, latitude and thermal stability of roosts, but not phylogeny, affect rewarming rates of bats

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HIGHLIGHTS

- We examined ecological, behavioral and physiological drivers of rewarming rates of 45 bat species.
- After controlling for phylogeny, high basal metabolic rate was associated with rapid rewarming.
- Species that live at higher absolute latitudes, and in less thermally stable roosts, also rewarmed most rapidly.
- Results suggest some species rely on passive means to reduce costs of rewarming, but others rely on faster metabolism as an alternative.
- This reinforces the importance of local climate, physiology, and behaviour in the proliferation of heterothermic endotherms

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ABSTRACT

Torpor is an adaptation that allows many endotherms to save energy by abandoning the energetic cost of maintaining elevated body temperatures. Although torpor reduces energy consumption, the metabolic heat production required to arouse from torpor is energetically expensive and can impact the overall cost of torpor. The rate at which rewarming occurs can impact the cost of arousal, therefore, factors influencing rewarming rates of heterothermic endotherms could have influenced the evolution of rewarming rates and overall energetic costs of arousal from torpor. Bats are a useful taxon for studies of ecological and behavioral correlates of rewarming rate because of the widespread expression of heterothermy and ecological diversity across the >1200 known species. We used a comparative analysis of 45 bat species to test the hypothesis that ecological, behavioral, and physiological factors affect rewarming rates. We used basal metabolic rate (BMR) as an index of thermogenic capacity, and local climate (i.e., latitude of geographic range), roost stability and maximum colony size as ecological and behavioral predictors of rewarming rate. After controlling for phylogeny, high BMR was associated with rapid rewarming while species that live at higher absolute latitudes and in less thermally stable roosts also rewarmed most rapidly. These patterns suggests that some bat species rely on passive rewarming and social thermoregulation to reduce costs of rewarming, while others might rely on thermogenic capacity to maintain rapid rewarming rates in order to reduce energetic costs of arousal. Our results highlight species-specific traits associated with maintaining positive energy balance in a wide range of climates, while also providing insight into possible mechanisms underlying the evolution of heterothermy in endotherms.

1. Introduction

Endothermic animals defend a constant, high body temperature (T_b) via endogenous, metabolic heat production, which can allow for sustained activity across a range of conditions. However, maintaining an elevated T_b is energetically expensive, especially during cold weather, and can become challenging during periods of low resource availability [1]. To offset these high energy demands, many endotherms employ facultative heterothermy or torpor [2]. Torpor is characterized by a controlled reduction of T_b, metabolic rate (MR), and other physiological functions, greatly reducing energy consumption [2]. Short bouts of torpor during certain parts of the day (i.e., daily torpor) and/or longer bouts at specific times of year (i.e., seasonal torpor or hibernation) allow endotherms to maintain positive energy balance across a range of environmental conditions and timescales, and can also result in other ecological benefits (reviewed by Geiser and Brigham [3]).

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Bouts of torpor can be separated into three phases: 1) the cooling phase, during which an individual decreases T_b and MR to a new, lower set-point, 2) the torpid phase, during which the individual defends a reduced T_b set-point and torpid metabolic rate (TMR, which can be less than 1% of resting MR) [4], and, 3) the warming or arousal phase, during which the individual actively terminates the torpor bout and rewarms to normothermic T_b. The arousal phase is considered one of the major disadvantages of heterothermy because rewarming from torpid to euthermic T_b is energetically expensive and requires extensive heat generation capacity [2,5]. High arousal costs negate potential energy savings of short torpor bouts, and therefore may represent an important factor in the cost-benefit tradeoff influencing torpor expression. Ultimately, these costs could represent a substantial portion of the long-term energy budget. Thus, mechanisms for mitigating costs of arousing from torpor are likely important drivers of the ecology, behavior, and life histories of heterothermic endotherms.

Somewhat counter-intuitively, rapid rewarming is less energetically demanding than rewarming slowly because the need to balance heat production with heat loss to the environment is less costly over shorter time intervals [6]. This predicts that selection should favor rapid rewarming or, alternatively, other energy-saving mechanisms such as social thermoregulation or passive rewarming to minimize arousal costs. If arousal from torpor depends on metabolic heat production, heterothermic species with greater thermogenic capacity (potentially higher basal and/or summit metabolic rate) should be capable of rewarming more rapidly [7]. However, the evolutionary relationship between MR and rewarming rate remains unclear. Geiser and Baudinette [7] found a nearly perfect correlation between BMR and rewarming rate across all mammalian taxa but few subsequent analyses exist and, those studies that do have found equivocal patterns within a single taxon or group [8,9].

The lack of a consistent relationship between MR and rewarming rate could also reflect the fact that rewarming in many species is largely passive [10,11,12] and does not rely solely on metabolic heat production. For species employing passive strategies, the energetic costs associated with rewarming may be heavily influenced by behavioral and environmental factors that allow individuals to take advantage of external heat sources for passive rewarming [6,11,13]. The availability of solar radiation and fluctuations in ambient temperature (T_a) are important determinants of the energetic cost of rewarming [10,11,12,13]. Many heterothermic endotherms have limited exposure to sunlight and/or variation in natural T_a in their burrows, nests, or roosts (e.g., underground burrows, caves, well-insulated trees), minimizing opportunities for passive rewarming. In addition, variation in the rate at which heterothermic endotherms rewarm from torpor might also reflect local behavioral and physiological adaptation to different climatic regimes. Many other energetic and physiological traits vary along latitudinal gradients [14–17], including BMR, capacity for non-shivering thermogenesis, heterothermy index (i.e., continuous metric of heterothermy [18]) and thermoregulatory scope (i.e., range of body temperatures exhibited by a species, mean T_b − minimum T_b [17]). Species residing at higher latitudes demonstrate greater thermogenic capacity (i.e., higher MR [15] and greater non-shivering thermogenesis [16]) to cope with unpredictable, occasionally extreme changes in environmental conditions. Temperate heterotherms might also exhibit faster rewarming rates to reduce costs of arousal when T_a is cold and access to passive heat sources is limited.

Social thermoregulation is another behavioral strategy that could influence rewarming rate. Some heterotherms huddle with conspecifics to reduce heat loss and/or increase T_a of their immediate microclimate [19,20]. Huddling is common in species that hibernate, roost, or nest in enclosed burrows where opportunities for passive heating are reduced. If groups of individuals can share thermoregulatory costs or reduce heat loss by huddling, this could reduce selection pressure favoring rapid warming. On the other hand, solitary species or those in smaller groups may depend on endogenous thermogenic capacity and rapid rewarming to keep the cost of arousal low [6,21].

Bats are a useful model taxon for comparative studies of heterothermy and rewarming. They are among the most ecologically diverse vertebrates and many species from both temperate and tropical regions employ daily and/or seasonal torpor, with some temperate species dependent on months of hibernation for over-winter survival [22]. Different bat species roost in a range of habitats, from caves and mines with high thermal stability, to tree hollows with moderate thermal stability to shedding bark or exposed foliage with high thermal variability. In addition, there is enormous variation in the potential for social thermoregulation among bats with some species roosting in large colonies of up to hundreds of thousands or millions of individuals and others roosting solitarily for most or all of their annual cycle [23]. This variation in ecology and behavior provides an excellent opportunity to test hypotheses about the evolution of rewarming rates in heterothermic endotherms.

We used comparative analyses to assess how physiological, behavioral and environmental variation affect rewarming rates of bats. First, we tested the hypothesis that metabolic rate is associated with rewarming rate in bats and predicted that species with higher BMR would exhibit faster maximum rewarming rates. Second, we tested the hypothesis that latitudinal variation in climate affects the evolution of rewarming rates. We predicted that bat species living at higher, temperate latitudes might be capable of faster maximum rewarming rates compared to low latitude species because of selective pressure imposed by colder, less predictable environmental conditions. Finally, we tested the hypothesis that roosting behavior affects the evolution of rewarming rates and predicted that species living in smaller groups and in less thermally stable roosts would exhibit the highest rewarming rates because these species have limited opportunities for passive rewarming and, therefore, should have faced selection pressure favoring rapid rewarming.

2. Methods

2.1. Field measurements of rewarming rate

We collected data for silver-haired (*Lasionycteris noctivagans*) and northern long-eared bats (*Myotis septentrionalis*) at the Sandilands Forest Discovery Centre in Manitoba, Canada (49.67°N, 95.90°W), from July 27th to August 1st, 2012 and 2014. Bats were captured using mist nets (12 m by 6 m), held in cloth bags and transported less than 1 km on foot to a nearby field laboratory. Here, bats were kept in their holding bags in a quiet room with screen-windows, under natural photoperiod (16 h light, 8 h dark) and natural T_a (minimum 11 °C–maximum 33 °C) for up to 24 h. At least two times a day, bats were provided with water, using a disposable pipette but were not fed because captivity was so brief.

As part of a concurrent respirometry study, every night up to four bats were placed in 100 mL transparent, acrylic chambers within a temperature-controlled cabinet set at 15 °C (i.e., well below the lower critical temperature) to encourage bats to enter torpor. The following day, between 13:00 and 22:00 individuals were removed from their chambers one at a time, and T_b was measured immediately (T_{b1}), by inserting a lubricated, 1 mm diameter thermocouple approximately 3 mm into the rectum until the reading was stable. After the first measurement, the bat was placed in a handling bag for approximately 5 min to minimize handling stress, after which a second T_b measurement was recorded (T_{b2}). Rewarming rate was calculated by subtracting T_{b1} from T_{b2} and dividing by the time interval between the two T_b measurements to give a rate in °C/min. Following T_b measurements, bats were weighed, provided water with a disposable pipette and released at the site of capture at dusk. These procedures and fieldwork were conducted under a Manitoba Conservation Wildlife Scientific Permit and were approved by the University of Winnipeg Animal Care Committee.