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Title

Daily torpor in birds and mammals: past, present, and future of the field

Running title

Daily torpor in birds and mammals

Authors

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Abstract

Torpor is an incredibly efficient energy-saving strategy that many endothermic birds and mammals use to save energy, by lowering their metabolic rates, heart rates, and typically body temperatures. Over the last few decades, the study of daily torpor—in which torpor is used for less than 24 hours per bout—has advanced rapidly. The papers in this issue cover the ecological and evolutionary drivers of torpor, as well as some of the mechanisms governing torpor use. We identified broad focus areas that need special attention: clearly defining the various parameters that indicate torpor use and identifying the genetic and neurological mechanisms regulating torpor. Recent studies on daily torpor and heterothermy, including the ones in this issue, have furthered the field immensely. We look forward to a period of immense growth in this field.

Introduction

Animals that experience periods of low or unpredictable energy supply have evolved diverse behavioral and physiological strategies to survive them. One such strategy is the use of daily torpor, an energy saving mechanism that allows animals to minimize metabolic expenditure for a few hours at a time by lowering their metabolic rates and heart rates, and typically also body temperatures (Ruf and Geiser 2015, see discussion on “hot torpor” below). The study of pronounced heterothermy has long focused more on hibernation (*i.e.*, multi-day torpor, used by ground squirrels and insectivorous bats for instance (Barnes 1989; Currie et al. 2018)) than on daily torpor (shorter bouts of torpor <24 hours used by many mammal and bird species (Lasiewski 1963; McKechnie and Lovegrove 2002; Brigham et al. 2006; McKechnie and Mzilikazi 2011; Shankar et al. 2020)) or large daily body temperature variations that do not qualify as torpor (Hetem et al. 2016; Levesque et al. 2023 unpublished).

Research on daily torpor, which in comparison to hibernation began rather late around the 1960's (e.g., Lasiewski 1963; Tucker 1966), has progressed quickly and expanded rapidly across study systems in the last few decades. This was facilitated by recent advancements in a variety of technologies, including increasingly portable respirometry equipment, higher-resolution thermal cameras, miniaturized heart rate loggers or radio transmitters, small data loggers on live animals that can record a range of physiological information in real-time, and minimally invasive approaches such as quantitative magnetic resonance (QMR) scanners that can provide body composition data for live animals.

Given these developments, we conducted a symposium titled “Daily torpor across birds and mammals: Recent progress and how do we advance the field?”. We brought together a mix of early-career and more established researchers in the field of daily torpor together to share ideas and perspectives on how this field has progressed and to discuss better ways to integrate methods and ideas to advance the field. Based on our assessment of the current state of the field, we believe that the time is now for a synthetic and cohesive conversation that addresses

the gaps and shared approaches to advance our understanding of daily torpor. The study of daily torpor has branched off in many directions. New findings and interdisciplinary studies highlight the need for greater collaboration between researchers investigating mammalian torpor and their counterparts studying avian torpor, and between ecologists, physiologists, and researchers in, for example, the fields of neuroscience and genomics. In this issue, researchers who study diverse taxa across birds and mammals globally (from tenrecs and primates, to hummingbirds and bats; in Africa, North and South America, Asia, Europe, and Australia) present a brief history of daily torpor research in their study system(s) over the past few decades, examine the current state of knowledge, and touch on the main unanswered questions in the field. In this introduction to the issue, we summarize key findings from papers and present a summary of the most pressing questions that remain unanswered, which symposium participants helped collate.

Heterothermy or torpor?

Torpor has been variously defined, but it usually involves a decrease in metabolic rate and heart rate, and, below the thermoneutral zone, usually a reduction in body temperature. Many factors make comparing torpor or heterothermy across taxa complicated with regard to what encompasses 'shallow torpor' (e.g., an intermediate drop in metabolism and maybe body temperature), 'deep torpor' (a drop in metabolism and body temperature to minimum possible levels for the species given ambient temperature), or simply other forms of circadian body temperature fluctuations (e.g., 1-2°C drop in body temperature during sleep). Torpor is often described as being routine, seasonal, or having strong circadian/circannual rhythms. It is sometimes, especially in free-living animals, evaluated with just body temperature or surface temperature measurements; or by measurements of only metabolic rates or heart rates, and more rarely with all three measurements simultaneously. As a consequence, the parameters used to identify torpor vary widely across studies. These considerations have been addressed in a number of reviews on the topic (Boyles et al. 2013; Ruf and Geiser 2015; Levesque et al. 2017;

Geiser 2021; Levesque et al. 2023 unpublished). To help make data comparable across studies, ideally, at least a combination of two variables such as metabolic rate and body temperature would be measured simultaneously. In situations where this is not possible (such as in free-ranging animals) then great care should be taken in interpreting the results as well as in attempting to determine metabolic states (such as torpor) from body temperature alone (Currie et al. 2022).

Additional complications in the study of torpor come from differentiating between circadian decreases in body temperature or metabolism, and torpor, and from measuring temperature under vastly different conditions, both internal and external to the organism. Differentiating torpor from regular circadian decreases in metabolism can be tricky. Some metabolic states are clearly distinct and exclusive. For instance, metabolic rates during daily torpor and hibernation differ substantially even under comparable environmental conditions, indicating that they are different metabolic states (Staples 2016; Currie et al. 2022). However, some species—ranging from mammals to hummingbirds—display a diversity of intermediate metabolic states that fall on a continuum between daily torpor and circadian heterothermy (Walker et al. 1979; Berger 1984; Shankar et al. 2022; Levesque et al. 2023 unpublished; Nowack, Mzilikazi, et al. 2023; Nowack, Stawski, et al. 2023)

The frequency and depth of torpor bouts can also differ between laboratory and field measurements. An animal's capacity to use torpor can be measured under laboratory conditions, but predicting how they would use it under natural conditions can be difficult (Geiser et al. 2000). Both situations yield useful information in understanding a species' capacity for torpor, and its practice of using torpor under natural conditions. In captivity, individuals of sugar gliders (*Petaurus breviceps*), owl-night-jars (*Aegotheles cristatus*) and long-eared bats (*Nyctophilus geoffroyi*) tend to avoid torpor or to use it less frequently, for shorter durations, and less deeply than free-living animals (Geiser et al. 2000, 2007). In

contrast, among common noctule bats (*Nyctalus noctula*), non-reproductive males tend to use torpor similarly and frequently both in captivity and in the wild; while reproductive males use torpor in the lab and drastically reduce torpor use in the wild (Keicher et al. 2023). These measurements in captive and free-ranging individuals hence often provide different subsets of information. The issue is further complicated by different definitions being used for large and small mammals and birds. The term heterothermy, for example, is often used to describe torpid states in small mammals, but also includes variations in daily body temperature/metabolic amplitudes in non-torpid large mammals (Hetem et al. 2016) and birds (rest-phase hypometabolism; see Levesque et al. 2023).

Measuring torpor with/without metabolic measurements

Given that torpor can occur at both high and low ambient temperatures and thus does not always correspond to a marked decrease in body temperature, how can torpor be diagnosed in free-ranging animals without metabolic rate measurements (Canale et al. 2012; O'Mara et al. 2018; Reher and Dausmann 2021)? There is no precise model across all heterothermic species that can use body temperature or its gradient with ambient temperatures to predict metabolic rates in torpor (Grimpo et al. 2013; Reher et al. 2018). Consequently, the development of small, field-friendly, and inexpensive devices for heart rate or highly sensitive activity loggers would help us measure and assess proxies of metabolic rate in free-living animals (where doing so is ethical and safe). The lack of a universal model for how body temperature correlates with metabolic state is another reason why comparisons of carefully collected laboratory data and field observations with a variety of measures is essential across a diversity of taxa (Keicher et al. 2023). Comparisons evaluating the relationships between these measures are relevant to both tropical and sub-tropical heterotherms but are likely most easily tested in species with a good record of torpor use at high ambient temperatures in the laboratory (*e.g.*, pygmy-possums, bats, spiny mice). Some attempts (in common noctule bats *Nyctalus noctula*, Hurme et al. unpublished) have been made to derive torpor patterns based on calibrated and fine-scale

accelerometers. These activity loggers cannot yet be used to quantify energy expenditures especially during inactive periods (Green et al. 2009), but can potentially help identify if an animal is torpid or in another specific activity state and achieve rough energy expenditure estimates if the accelerometers are calibrated in the laboratory with parallel metabolic rate measurements (Wilson et al. 2008).

Eco-evolutionary drivers for torpor use

Environmental factors

In the last few decades, it has become apparent that torpor has more functions than to reduce the animal's energetic needs when it is faced with low ambient temperatures or food availability (Geiser and Brigham 2012; Nowack et al. 2017). Torpor may also be used in response to high ambient temperatures, high normothermic energetic demands, low availability of water, and environmental disasters (*e.g.*, fires, floods), or diminished foraging options (*e.g.*, Stawski et al. 2015; Reher and Dausmann 2021). These diminished foraging options could be in response to changing food availability (Lovegrove 2000), high predation pressures (Stawski and Geiser 2010) or even high interspecific competition, such as in golden spiny mice which seem to increase torpor use and diurnalism to avoid competition with nocturnal common spiny mice (Levy et al. 2012). Extensive reviews have been written covering a range of these factors (Geiser and Brigham 2012; Nowack et al. 2017; Geiser 2021). These other drivers of torpor have changed our understanding of the functions of torpor. As the discovery of torpor use at high ambient temperatures (hot torpor) as well as torpor use in response to natural disasters are relatively new discoveries, we discuss them briefly here.

Torpor at high ambient temperatures (Hot torpor): More and more animals have been found to use torpor at high ambient (and body) temperatures—not only in the tropics and sub-tropics but also in temperate zones (Song et al. 1997; Bondarenko et al. 2014; O'Mara et al. 2017, 2018; Reher et al. 2018; Reher and Dausmann 2021; Keicher et al. 2022). For instance, Malagasy bats

(*Macronycteris commersoni*) are able tolerate hyperthermy on hot days, with body temperatures over 42.9 °C, while also using torpor by decreasing their metabolic rate to about 17% of euthermic metabolic rates (Reher and Dausmann 2021). While we have a good understanding about the physiology of torpor when animals use torpor at cooler temperatures (Jastroch et al. 2016; Geiser 2021), we know little about the underlying physiological processes involved when animals lower their metabolism and heart rate at high ambient temperatures. Torpor at high temperatures could potentially help animals to deal with more frequent occurrences of temperature extremes associated with climate change (Lovegrove et al. 2014). But to fully assess this potential, we need to test whether more species are capable of high-temperature torpor. This should be confirmed in the wild to verify that they actually use high-temperature torpor in natural conditions. Once such species are identified, we can investigate the underlying physiological processes that allow for lowered metabolic rates at high body temperatures. It is possible that all heterothermic species exposed to high temperatures in the field can show such a pattern of metabolic inhibition at high body temperature—and could species that live in historically colder habitats use hot torpor to the same extent that we observe in species in warm areas? Some promising starting points are other bat species in both tropical and temperate zones, but more mammals and birds should be investigated from this perspective.

Environmental disasters: Torpor has been evaluated in the context of various environmental disasters and found important. These include floods, storms, droughts, heat waves, and fires (Zervanos and Salsbury 2003; McKechnie and Mzilikazi 2011; Geiser and Brigham 2012; Nowack et al. 2015, 2016, 2017; Barak et al. 2019). Torpor has even been proposed to help facilitate island colonization (Nowack and Dausmann 2015), and thought to have allowed mammals to survive the Cretaceous-Palaeogene (K-Pg) boundary (Lovegrove et al. 2014). Under all of these scenarios, torpor can allow animals to decrease their energetic needs under difficult environmental conditions that could either limit food availability or make sustaining normothermic energy levels very challenging. Very limited background information exists on

the use of torpor during floods: these are essentially restricted to two accidental observations (Maddocks and Geiser 2007; Barak et al. 2019); but this is likely an ecologically significant behavior (Geiser 2021). The best potential species to further study this in might be rodents and small dasyurids, though it is clearly very difficult to predict and study torpor during natural floods. More is known about torpor use during fires, but the work is currently restricted to Australian species (Stawski et al. 2015; Nowack et al. 2016). For detailed reviews of torpor during environmental disasters, refer to Geiser and Brigham (2012) and Nowack et al. (2017). Gathering data on the use of torpor in response to natural disasters is a challenging endeavor, but more data are needed to fully understand the eco-evolutionary drivers of torpor use.

Ecology and timing of torpor use

Reproductive, developmental, and seasonal changes in torpor: The role of heterothermy during development and reproduction in endotherms is a poorly explored subject. A broad comparative study of the age at which endothermy develops (Price and Dzialowski 2018) and the extent to which heterothermy is tolerated across birds and mammals would provide a powerful way to assess the development and perhaps evolution of heterothermy and endothermy (Lovegrove 2017). Torpor is used by diverse mammals during development—including species for which torpor use is not found in adults—often when they are around half the size of adults, are inexperienced and have a high heat loss (McAllan and Geiser 2014, 2018). Unfortunately, many of these data were not gathered systematically and are based on small sample sizes. In the field, most information on torpor during development is largely anecdotal (but see Klug and Barclay 2013). In the laboratory some good physiological data are available, but not on many taxa of different body masses and mainly on altricial species (Wacker et al. 2017). However, the precocial king quail (*Coturnix chinensis*) seems to be able to use shallow torpor in the early postnatal phase of development (Geiser et al. 2006, 2019; Geiser 2008; Aharon-Rotman et al. 2020).

An interesting related question is the role that torpor plays in reproductive adults. Testosterone inhibits torpor in males of many species, including Afrotropical pouched mice (*Saccostomus campestris*), golden-mantled ground squirrels (*Callospermophilus lateralis*), and European hamsters (*Cricetus cricetus*) (Barnes et al. 1986; Darrow et al. 1988; Mzilikazi and Lovegrove 2002). Photoperiod can compound the effects of reproductive hormones on torpor: estradiol inhibited torpor in hibernating female hamsters, with hamsters hibernating in long days showing more torpor inhibition than those in short days (Darrow et al. 1988). Studies on hummingbirds have found that incubating females tend to avoid torpor, seemingly prioritizing keeping their eggs and chicks at relatively stable temperatures (Calder 1973; Smith et al. 1974; Eberts et al. 2023), whereas pregnant marsupial mulgaras (*Dasycercus cristicauda*) use daily torpor routinely (Körtner et al. 2008). While altricial bird species whose adults use torpor would be an obvious group to explore these questions further, these are important questions across all mammals and birds, including small precocial birds (Aharon-Rotman et al. 2020; Geiser 2021).

Torpor use can change over seasons or depending on ambient conditions (Eberts et al. 2021). The proximate factors triggering torpor entry (*e.g.*, fat stores, circadian rhythms, ambient temperature) can also vary dramatically across seasons. Similarly, resource availability may fluctuate, and its availability and predictability can influence torpor use (McAllan and Geiser 2014). Animals that use torpor during the reproductive phase often inhabit unpredictable environments or reproduce at least partially during the winter when food availability is lower or more unpredictable (McAllan and Geiser 2014). In addition, reproduction can suppress torpor use (see above), and is often seasonally timed to coincide with highest resource abundance and most favorable temperature conditions. Disentangling these effects is challenging (Becker et al. 2013). Thus, to understand how torpor use is influenced by ecological and environmental factors, studies are needed that measure environmental and physiological parameters across seasons in combination with laboratory studies to disentangle some of the

seasonal effects. Keicher et al. (2023) found that non-reproductive male bats used torpor frequently whether they were captive or free-living, while reproductive males reduced torpor use in the field, but used torpor frequently under laboratory conditions (with ambient temperature conditions mimicking field temperatures). Keicher et al. (2022) studied female bats (*Nyctalus noctula*) in the laboratory under simulated natural temperatures and found that non-reproductive females used torpor throughout the experiment, while pregnant females varied widely in their torpor use, ranging from torpor to normothermy or a combination of the two. These kinds of experiments can be used to evaluate the effects of reproductive status on torpor under various temperature conditions, but since season and reproductive status are often correlated, they are more difficult to decouple.

Migration: Migration, particularly aerial migration, is a highly energy-intensive life history strategy. Not only is flying itself expensive, but periods of stopover and refueling also consume large amounts of energy—sometimes twice as much energy as migratory flight itself (Hedenström and Ålerstam 1997). Studies on birds have found that even small body temperature decreases by the use of relatively shallow torpor can help save up to 30% of the energy that birds would otherwise use during migratory stopovers (Wojciechowski and Pinshow 2009; Carere et al. 2010; McKechnie et al. 2023). These studies were done in blackcaps (*Sylvia atricapilla*), garden warblers (*Sylvia borin*), and icterine warblers (*Hippolais polyglotta*); in the warblers, body temperatures dropped by 10°C at night (Carere et al. 2010). Despite these studies, we still have limited information on torpor use during migration and the role it may play in stopover ecology and refueling (Carpenter and Hixon 1988; Powers et al. 2003; Hou and Welch 2016; Zenzal and Moore 2016; Clerc and McGuire 2021; Eberts et al. 2021). We also have very limited knowledge of how body condition may influence torpor expression, and even less about how this varies within and among migrating species, or across species distributions. Another area that requires study involves how migrating birds and mammals' energy use are affected by climate change and potential food deserts on their migratory route. McGuire et al.

(2023) summarize some of the recent findings on torpor-assisted migration, laying out a conceptual framework that can help integrate energetic considerations of torpor and migration. For instance, they suggest that for animals that do not hibernate (*e.g.*, all but one bird species), migration might be a useful strategy for avoiding unfavorable conditions. They also propose ways in which we can advance the study of migratory animals that use torpor.

Costs of torpor: Torpor seems to be a trade-off between its various benefits and a variety of potential costs. In some species, for instance, it seems incompatible with molting or structural growth (Hiebert 1993; Mahlert et al. 2018). Daily torpor could make the animal susceptible to predation because they are often unresponsive or very sluggish in torpor. However, the various costs of daily torpor have only very rarely been tested experimentally. From a few studies in mammals (mostly hibernators), we know that some potential costs include immune impairment and predation vulnerability (Bouma et al. 2010), although it may also be used for predator avoidance (Bieber and Ruf 2009). A daily heterotherm (the Djungarian hamster *Phodopus sungorus*) emerges from torpor and sleeps and shows many signs of recovering from sleep deprivation in this period, suggesting this as a physiological cost to the use of torpor (Palchykova et al. 2002, 2006). Another potential cost of torpor, at least among hibernating animals, is telomere shortening (Nowack et al. 2019; Viblanc et al. 2022). However, in Djungarian hamsters (*Phodopus sungorus*) that use daily torpor, telomere length increased, likely during arousals (Turbill et al. 2012). To avoid these potential negative effects on fitness, many species limit the torpor use to outside the reproductive period of the annual cycle (Bartness et al. 1989; Fietz et al. 2004). However, some species still use torpor during reproduction, often even increasing reproductive success and likelihood of survival during the reproductive period with the use of torpor (McAllan and Geiser 2014). In ruby-throated hummingbirds (*Archilochus colubris*), for example, breeding success among males may be correlated with leaner body condition (promoting agility and enhancing competitiveness or mate attraction). In these situations, the maintenance of larger energy reserves necessary to

remain normothermic throughout nighttime inactive periods is contradicted by the drive for reproductive success and torpor, as a mechanism of surviving inactive periods equipped with low energy reserves, may be favored (Eberts et al. 2021).

The evolution of torpor

To better understand how torpor evolved, we need broader comparative studies that assess the genetic pathways involved in bird and mammal heterothermy (shared, convergent, or divergent). One approach is to perform ancestral state reconstruction analyses to evaluate the likelihood of heterothermy being ancestral rather than derived across endothermic vertebrates. Nowack et al. (2023) performed these analyses for mammals and found based on currently available data, that all three torpor types they considered—daily torpor, prolonged torpor, and hibernation—were equally likely ancestral states for mammals. Seasonal and non-seasonal torpor use seemed equally likely to be the ancestral condition. This supports the hypotheses from previous work that endothermy might have evolved through stepwise increases in metabolic rates, via some form of heterothermy (Crompton et al. 1978; Lovegrove 2012, 2017; Geiser et al. 2017). However, it should be noted that these analyses are sensitive to the types of data that are available and, as existing datasets are biased towards Holarctic hibernators, these results are likely to change with the inclusion of more data from the sub-tropics and tropics (Nowack, Stawski, et al. 2023).

Among heterotherms, seasonal heterotherms from temperate or arctic regions are best known for their use of torpor. However, recent evidence shows that, following global patterns of biodiversity, many more heterotherms live in tropical or warm and arid regions (Nowack et al. 2020). While previously their flexible torpor patterns were regarded as exceptions, when compared with predictable temperate zone torpor patterns, is it more likely that the ‘champions’ of torpor use, such as the Holarctic ground squirrels (Barnes 1989) are the exceptions. In birds, torpor appears to be more prevalent in phylogenetically older taxa, and

deep torpor is absent in passerines, with body temperatures staying relatively high. This lack of deep torpor in relatively derived taxa is perplexing, but McKechnie et al. (2023) suggest based on published data that perhaps the lipid composition of cell membranes might be a trade-off between tolerating low temperatures vs. high temperatures (Arnold et al. 2011; Price and Dzialowski 2018), and hence being able to withstand hyperthermy might preclude the ability to use deep torpor or heterothermy below the thermoneutral zone.

Genetic pathways regulating torpor

What remains largely unknown in terms of the evolution and genetic pathways underlying torpor is what aspects of the genetic and physiological processes underlying heterothermy are shared between birds and mammals. For instance, circadian genes seem to be important in regulating daily torpor in mammals. Some gene expression information is known from mammalian daily torpor, but nothing is known about the genetic pathways involved in avian torpor. Tissue-specific gene expression data from normothermic birds and birds in torpor, across multiple taxa could be collected in a way comparable to how it has been done in some mammals (Williams et al. 2011; Schwartz et al. 2013; Bogren et al. 2017; Andrews 2019; Goropashnaya et al. 2020). These genetic traits as well as physiological traits could then be compared across birds, non-avian reptiles, and mammals to better assess the evolution of endothermy and heterothermy.

Proximal mechanisms regulating torpor use

Torpor is a highly controlled energy-saving strategy, as evidenced by its nuanced use under a variety of ecological and environmental conditions. What proximate factors tell an animal to use or avoid torpor at any particular time point? Proximate factors that indicate time (clock genes or circadian functions), hormones that indicate energy levels or reproductive states (adipostat indicators such as leptin and ghrelin; testosterone/estrogen), gene expression to lower metabolic function, and protective mechanisms to prevent organ damage must all work together to initiate, maintain, and exit torpor (Geiser et al. 1998; Gluck et al. 2006; Cubuk, Kemmling, et

al. 2017; Ikeno et al. 2017; Eberts et al. 2019). Much more of this work has been conducted on hibernators than in daily heterotherms, but we summarize some of what is known, as well as the bigger gaps in knowledge, below.

Adipostat control and the role of leptin in torpor

Energy stores and indicators of energy levels clearly have important roles to play in regulating torpor use. Among mammals (e.g. mice *Mus musculus* and golden-mantled ground squirrels *Callospermophilus lateralis*), fasting can increase circulating ghrelin levels and induce torpor, and administering ghrelin deepens torpor (Gluck et al. 2006). Conversely, administering leptin can reduce daily torpor expression in animals like hamsters (*Phodopus sungorus*) and marsupial dunnarts (*Sminthopsis macroura*) (reviewed in Geiser 2021). In hummingbirds, fat thresholds seem to be the proximate triggers for torpor entry (Hiebert 1992; Powers et al. 2003; Eberts et al. 2021). These thresholds also change across seasons, switching from about 5% body fat in the non-migratory season (Powers et al. 2003) to around 30% during pre-migratory fattening (Eberts et al. 2021). Ambient temperature also seems to affect this threshold, and it is likely that sex does as well (Eberts et al. *unpublished*). However, administering avian leptin does not seem to have any effect on torpor use, fat mass, or food intake in ruby-throated hummingbirds (*Archilochus colubris*), and leptin resistance does not seem to help hummingbirds fatten prior to migration (Rossi and Welch 2023). What still remains somewhat obscure is how the environmental, ecological, and physiological factors for torpor initiation (and arousal) are integrated to result in observed patterns of torpor use. Do all hummingbirds, and other mammalian and avian daily heterotherms, use torpor when they deplete endogenous energy levels to particular, seasonally dependent levels? Expression of spontaneous torpor (when food is freely available) does not support that interpretation, at least from the few species studied, compared to those under food shortage conditions. It is also unclear whether the adipostat threshold is adjusted or abandoned, to allow for torpor use at relatively high fat levels during migration, winter, or while nesting. To answer these questions, we would need detailed body

composition measurements (*e.g.*, quantitative magnetic resonance or QMR) at torpor initiation (especially repeated within individuals) across more mammal and bird species across seasons and at different life history stage contexts (Eberts et al. 2021). Additionally, measuring endocrine signaling molecule levels prior to and at torpor initiation would be a helpful indicator of how endocrine regulation of torpor may occur.

Neural and endocrine mechanisms regulating torpor

The mechanisms by which the brain regulates torpor use in mammalian hibernators have been relatively well-studied compared to those that regulate avian or mammalian daily torpor (Jastroch et al. 2016). We know that in heterothermic mammals, the suprachiasmatic nucleus in the hypothalamus helps regulate the timing of torpor, and that the hypothalamus remains active throughout torpor/hibernation to control thermoregulation, hormones, and the timing of torpor (Bratincsák et al. 2007; Schwartz et al. 2013; Cubuk, Kemmling, et al. 2017; Cubuk, Markowsky, et al. 2017). The hippocampus has also been implicated in regulating mammalian hibernation: it loses activity last during transition into hibernation and regains it first upon arousal (Drew et al. 2007). The cerebellum controls motor coordination in both birds and mammals and controls unconscious posture adjustments and occasional vocalizations in hibernating mammals, indicating its potential involvement in torpor/hibernation (Tessier et al. 2019). On the other hand, few experiments have been done to determine the neural regulation of avian torpor. Considering the vast disparities between mammalian and avian brain architecture, it is reasonable to assume that mammals and birds may regulate torpor via the central nervous system differently. The finding that leptin does not seem to play a role in torpor in hummingbirds, while it does in mammals, also supports this assertion (Rossi and Welch 2023). Ghrelin is another indicator that birds and mammals have evolved very different regulatory pathways independently—it works very differently in birds and mammals (Goymann et al. 2017; Lupi et al. 2022). Given these differences, what neuroendocrine factors (*i.e.*, energy status signaling molecules and pathways) control the adipostat torpor threshold and its changes

across birds and mammals? What pathways coordinate and regulate the changes that occur with torpor use across organs? And are hot torpor and other forms of heterothermy regulated similarly? To address this gap, we would need gene expression data of various brain regions in heterothermic birds and mammals to determine whether certain regions, like the hypothalamus/hippocampus/cerebellum, are expressing relevant genes during torpor; detailed imaging experiments to identify neural regions and pathways that are associated with torpor entry; and perhaps also real-time imaging of bird brains during torpor such as with functional Magnetic Resonance Imaging (fMRIs). Some promising taxa that would be good starting points for comparative studies include animals that frequently use daily torpor (*e.g.*, hummingbirds, nightjars, Djungarian hamsters). Similar questions are also still largely unanswered when comparing tropical/sub-tropical and temperate mammal species.

Conclusion

Given the diversity of study systems in which daily torpor occurs, many different approaches, measures, and techniques have been developed to study torpor patterns. The papers in this issue cover ecological and evolutionary drivers of torpor, as well as some of the proximal mechanisms governing torpor use. We identified four broad focus areas over the course of the symposium.

1. The definitions of torpor are arbitrary, and sometimes contradictory. This is a tough problem to solve, but we advocate for presenting more raw data, or at least making them more accessible, to allow for re-analyses in different contexts, as well as including clear torpor definitions in each paper.
2. Many of our perceptions of what torpor is and how it is defined come from “champion hibernators” at high latitudes that use hibernation quite predictably, consistently, and deeply (Florant and Heller 1977; Heller et al. 1977; Walker et al. 1977), relative to the diversity of ways in which torpor is more commonly used. This has led to the torpor variable and patterns of some taxa being set as the standards, whereas others that use torpor in different ways being seen as “weird” torpor users. However, based on the number of species

in the tropics and sub-tropics now known to use torpor, our perceptions of what is the rule and what are the exceptions likely need to change (Nowack et al. 2020; Nowack, Stawski, et al. 2023).

3. Almost nothing is known about the genetic basis for torpor regulation among daily heterotherms—this is a big unsolved question in the field.

4. Very little is known about neural and endocrine regulation of torpor among daily heterotherms, or how these pathways differ between daily heterotherms and hibernators. Some recent studies on mice have identified specific neuronal pathways that are crucial for torpor entry (Hrvatin et al. 2020), but there is no indication that these pathways are evolutionarily conserved or widespread.

So much progress has been made in recent years (as evidenced by the papers in this issue), yet so much remains to be learned. We stand at the precipice of a period of immense growth in this field and hope this issue can constructively guide future studies and facilitate their progress.

Author contributions

AS and KCW organized the symposium. All authors contributed forward-looking questions to the manuscript. AS drafted the manuscript, and all other authors commented on and approved the final manuscript. After the first two authors, authors' names are in alphabetical order by last name.

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Conflicts of Interest

The authors declare no conflicts of interest.

References

Aharon-Rotman Y, Körtner G, Wacker CB, Geiser F. 2020. Do small precocial birds enter torpor to conserve energy during development? *J Exp Biol* 223:jeb231761.

Andrews MT. 2019. Molecular interactions underpinning the phenotype of hibernation in mammals. *J Exp Biol* 222:jeb160606.

Arnold W, Ruf T, Frey-Roos F, Bruns U. 2011. Diet-independent remodeling of cellular membranes precedes seasonally changing body temperature in a hibernator. *PLoS One* 6:e18641.

Barak O, Geiser F, Kronfeld-Schor N. 2019. Flood-induced multiday torpor in golden spiny mice (*Acomys russatus*). *Aust J Zool* 66:401–5.

Barnes BM. 1989. Freeze avoidance in a mammal: Body temperatures below 0°C in an arctic hibernator. *Science* (80-) 244:1593–95.

Barnes BM, Kretzmann M, Licht P, Zucker I. 1986. The influence of hibernation on testis growth and spermatogenesis in the golden-mantled ground squirrel, *Spermophilus lateralis*. *Biol Reprod* 35:1289–97.

- Bartness TJ, Elliott JA, Goldman BD. 1989. Control of torpor and body weight patterns by a seasonal timer in Siberian hamsters. <https://doi.org/10.1152/ajpregu1989.257.1.R142> 257.
- Becker NI, Tschapka M, Kalko EKV, Encarnação JA. 2013. Balancing the energy budget in free-ranging male *Myotis daubentonii* bats. *Physiol Biochem Zool* 86:361–69.
- Berger RJ. 1984. Slow wave sleep, shallow torpor and hibernation: Homologous states of diminished metabolism and body temperature. *Biol Psychol* 19:305–26.
- Bieber C, Ruf T. 2009. Summer dormancy in edible dormice (*Glis glis*) without energetic constraints. *Naturwissenschaften* 96:165–71.
- Bogren LK, Grabek KR, Barsh GS, Martin SL. 2017. Comparative tissue transcriptomics highlights dynamic differences among tissues but conserved metabolic transcript prioritization in preparation for arousal from torpor. *J Comp Physiol B* 187:735–48.
- Bondarenko A, Körtner G, Geiser F. 2014. Hot bats: Extreme thermal tolerance in a desert heat wave. *Naturwissenschaften* 101:679–85.
- Bouma HR, Carey H V., Kroese FGM. 2010. Hibernation: the immune system at rest? *J Leukoc Biol* 88:619–24.
- Boyles JG, Thompson AB, Mckechnie AE, Malan E, Humphries MM, Careau V. 2013. A global heterothermic continuum in mammals. *Glob Ecol Biogeogr* 22:1029–39.
- Bratincsák A, McMullen D, Miyake S, Tóth ZE, Hallenbeck JM, Palkovits M. 2007. Spatial and temporal activation of brain regions in hibernation: c-fos expression during the hibernation bout in thirteen-lined ground squirrel. *J Comp Neurol* 505:443–58.
- Brigham RM, Woods CP, Lane JE, Fletcher QE, Geiser F. 2006. Ecological correlates of torpor use among five caprimulgiform birds. *Acta Zool Sin* 52:401–4.
- Calder WA. 1973. An estimate of the heat balance of a nesting hummingbird in a chilling climate. *Comp Biochem Physiol -- Part A Physiol* 46:291–300.
- Canale CI, Levesque DL, Lovegrove BG. 2012. Tropical heterothermy: does the exception prove the rule or force a re-definition? In: T. Ruf et al., editor. *Living in a Seasonal World* Berlin Heidelberg: Springer-Verlag. p. 29–40.

- Carere C, Costantini D, Fusani L, Alleva E, Cardinale M. 2010. Hypothermic abilities of migratory songbirds at a stopover site. *Rend Lincei* 21:323–34.
- Carpenter FL, Hixon MA. 1988. A new function for torpor- fat conservation in a wild migrant hummingbird. *Condor* 90:373–78.
- Clerc J, McGuire LP. 2021. Considerations of varied thermoregulatory expressions in migration theory. *Oikos oik.08178*.
- Crompton AW, Taylor CR, Jagger JA. 1978. Evolution of homeothermy in mammals. *Nature* 272:333–36.
- Cubuk C, Kemmling J, Fabrizius A, Herwig A. 2017. Transcriptome analysis of hypothalamic gene expression during daily torpor in Djungarian hamsters (*Phodopus sungorus*). *Front Neurosci* 11.
- Cubuk C, Markowsky H, Herwig A. 2017. Hypothalamic control systems show differential gene expression during spontaneous daily torpor and fasting-induced torpor in the Djungarian hamster (*Phodopus sungorus*). *PLoS One* 12:e0186299.
- Currie SE, Körtner G, Geiser F. 2022. Pronounced differences in heart rate and metabolism distinguish daily torpor and short-term hibernation in two bat species. *Sci Reports* 2022 12:1–10.
- Currie SE, Stawski C, Geiser F. 2018. Cold-hearted bats: Uncoupling of heart rate and metabolism during torpor at sub-zero temperatures. *J Exp Biol* 221.
- Darrow JM, Duncan MJ, Bartke A, Bona-Gallo A, Goldman BD. 1988. Influence of photoperiod and gonadal steroids on hibernation in the European hamster. *J Comp Physiol A* 163:339–48.
- Drew KL, Buck CL, Barnes BM, Christian SL, Rasley BT, Harris MB. 2007. Central nervous system regulation of mammalian hibernation: implications for metabolic suppression and ischemia tolerance. *J Neurochem* 102:1713–26.
- Eberts ER, Dick MF, Welch KC. 2019. Metabolic fates of evening crop-stored sugar in ruby-throated hummingbirds (*Archilochus colubris*). *Diversity* 11:1–12.
- Eberts ER, Guglielmo CG, Welch KC. 2021. Reversal of the adipostat control of torpor during

- migration in hummingbirds. *Elife* 10:2021.05.13.443997.
- Eberts ER, Tattersall GJ, Auger PJ, Curley M, Morado MI, Strauss EG, Powers DR, Soveral NC, Tobalske BW, Shankar A. 2023. Free-living Allen's hummingbirds (*Selasphorus sasin*) rarely use torpor while nesting. *J Therm Biol* 112:103391.
- Fietz J, Schlund W, Dausmann KH, Regelman M, Heldmaier G. 2004. Energetic constraints on sexual activity in the male edible dormouse (*Glis glis*). *Oecologia* 138:202–9.
- Florant GL, Heller HC. 1977. CNS regulation of body temperature in euthermic and hibernating marmots (*Marmota flaviventris*). *Am J Physiol Integr Comp Physiol* 232:R203–8.
- Geiser F. 2008. Ontogeny and phylogeny of endothermy and torpor in mammals and birds. *Comp Biochem Physiol A Mol Integr Physiol* 150:176–80.
- Geiser F. 2021. Ecological physiology of daily torpor and hibernation, *Fascinating Life Sciences* Cham: Springer International Publishing.
- Geiser F, Brigham RM. 2012. The other functions of torpor. In: Ruf T, Bieber C, Arnold W, Millesi E, editors. *Living in a Seasonal World* Berlin, Heidelberg: Springer Berlin Heidelberg. p. 109–21.
- Geiser F, Holloway JC, Körtner G. 2007. Thermal biology, torpor and behaviour in sugar gliders: a laboratory-field comparison. *J Comp Physiol B* 177:495–501.
- Geiser F, Holloway JC, Kortner G, Maddocks TA, Turbill C, Brigham RM. 2000. Do patterns of torpor differ between free- ranging and captive mammals and birds? In: Heldmaier G, Klingenspor M, editors. *Life in the Cold: Eleventh International Hibernation Symposium* Berlin: Springer Berlin Heidelberg. p. 95–102.
- Geiser F, Körtner G, Schmidt I. 1998. Leptin increases energy expenditure of a marsupial by inhibition of daily torpor. *Am J Physiol Integr Comp Physiol* 275:R1627–32.
- Geiser F, Stawski C, Wacker CB, Nowack J. 2017. Phoenix from the ashes: fire, torpor, and the evolution of mammalian endothermy. *Front Physiol* 8:842.
- Geiser F, Wen J, Sukhchuluun G, Chi QS, Wang DH. 2019. Precocious torpor in an altricial mammal and the functional implications of heterothermy during development. *Front*

Physiol 10:469.

Geiser F, Westman W, McAllan BM, Brigham RM. 2006. Development of thermoregulation and torpor in a marsupial: energetic and evolutionary implications. *J Comp Physiol B* 176:107–16.

Gluck EF, Stephens N, Swoap SJ. 2006. Peripheral ghrelin deepens torpor bouts in mice through the arcuate nucleus neuro peptide Y signaling pathway. *Am J Physiol Regul Integr Comp Physiol* 291:1303–9.

Goropashnaya A V, Barnes BM, Fedorov VB. 2020. Transcriptional changes in muscle of hibernating arctic ground squirrels (*Urocitellus parryii*): implications for attenuation of disuse muscle atrophy. *Sci Rep* 10:9010.

Goymann W, Lupi S, Kaiya H, Cardinale M, Fusani L. 2017. Ghrelin affects stopover decisions and food intake in a long-distance migrant. *Proc Natl Acad Sci* 114:1946–51.

Green JA, Halsey LG, Wilson RP, Frappell PB. 2009. Estimating energy expenditure of animals using the accelerometry technique: activity, inactivity and comparison with the heart-rate technique. *J Exp Biol* 212:471–82.

Grimpo K, Legler K, Heldmaier G, Exner C. 2013. That's hot: Golden spiny mice display torpor even at high ambient temperatures. *J Comp Physiol B Biochem Syst Environ Physiol* 183:567–81.

Hedenström A, Alerstam T. 1997. Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. *J Theor Biol* 189:227–34.

Heller HC, Colliver GW, Beard J. 1977. Thermoregulation during entrance into hibernation. *Pfùlgers Arch* 369:55–59.

Hetem RS, Maloney SK, Fuller A, Mitchell D. 2016. Heterothermy in large mammals: inevitable or implemented? *Biol Rev* 91:187–205.

Hiebert SM. 1992. Time-dependent thresholds for torpor initiation in the rufous hummingbird (*Selasphorus rufus*). *J Comp Physiol B* 162:249–55.

Hiebert SM. 1993. Seasonal changes in body mass and use of torpor in a migratory

- hummingbird. *Auk* 110:787–97.
- Hou L, Welch KC. 2016. Premigratory ruby-throated hummingbirds, *Archilochus colubris*, exhibit multiple strategies for fuelling migration. *Anim Behav* 121:87–99.
- Hrvatın S, Sun S, Wilcox OF, Yao H, Lavin-Peter AJ, Cicconet M, Assad EG, Palmer ME, Aronson S, Banks AS, Griffith EC, Greenberg ME. 2020. Neurons that regulate mouse torpor. *Nat* 2020 5837814 583:115–21.
- Ikeno T, Williams CT, Buck CL, Barnes BM, Yan L. 2017. Clock gene expression in the suprachiasmatic nucleus of hibernating arctic ground squirrels. *J Biol Rhythms* 32:246–56.
- Jastroch M, Giroud S, Barrett P, Geiser F, Heldmaier G, Herwig A. 2016. Seasonal control of mammalian energy balance: recent advances in the understanding of daily torpor and hibernation. *J Neuroendocrinol* 28:1–10.
- Keicher L, Shipley JR, Komar E, Ruczyński I, Schaeffer PJ, Dechmann DKN. 2022. Flexible energy-saving strategies in female temperate-zone bats. *J Comp Physiol B Biochem Syst Environ Physiol* 192:805–14.
- Keicher L, Shipley JR, Schaeffer PJ, Dechmann DKN. 2023. Contrasting torpor use by reproductive male common noctule bats in the laboratory and in the field. *Integr Comp Biol*.
- Klug BJ, Barclay RMR. 2013. Thermoregulation during reproduction in the solitary, foliage-roosting hoary bat (*Lasiurus cinereus*). *J Mammal* 94:477–87.
- Körtner G, Pavey CR, Geiser F. 2008. Thermal biology, torpor, and activity in free-living mulgaras in arid zone Australia during the winter reproductive season. *Physiol Biochem Zool* 81:442–51.
- Lasiewski RC. 1963. Oxygen consumption of torpid, resting, active and flying hummingbirds. *Physiol Zool* 36:122–40.
- Levesque DL, Breit A, Brown E, Nowack J, Welman S. 2023. Non-torpid heterothermy in mammals: another point along the homeothermy-hibernation continuum, Manuscript accepted at *Integrative and Comparative Biology*.

- Levesque DL, Menzies AK, Landry-Cuerrier M, Larocque G, Humphries MM. 2017. Embracing heterothermic diversity: non-stationary waveform analysis of temperature variation in endotherms. *J Comp Physiol B Biochem Syst Environ Physiol* 187:749–57.
- Levy O, Dayan T, Rotics S, Kronfeld-Schor N. 2012. Foraging sequence, energy intake and torpor: an individual-based field study of energy balancing in desert golden spiny mice. *Ecol Lett* 15:1240–48.
- Lovegrove BG. 2000. Daily heterothermy in mammals: coping with unpredictable environments. In: *Life in the Cold* Berlin, Heidelberg: Springer Berlin Heidelberg. p. 29–40.
- Lovegrove BG. 2012. The evolution of endothermy in Cenozoic mammals: a plesiomorphic-apomorphic continuum. *Biol Rev* 87:128–62.
- Lovegrove BG. 2017. A phenology of the evolution of endothermy in birds and mammals. *Biol Rev* 92:1213–40.
- Lovegrove BG, Canale C, Levesque D, Fluch G, Řeháková-Petrů M, Ruf T. 2014. Are tropical small mammals physiologically vulnerable to Arrhenius effects and climate change? *Physiol Biochem Zool* 87:30–45.
- Lupi S, Morbey YE, MacDougall-Shackleton SA, Kaiya H, Fusani L, Guglielmo CG. 2022. Experimental ghrelin administration affects migratory behaviour in a songbird. *Horm Behav* 141:105139.
- Maddocks T a., Geiser F. 2007. Heterothermy in an Australian passerine, the Dusky Woodswallow (*Artamus cyanopterus*). *J Ornithol* 148:571–77.
- Mahlert B, Gerritsmann H, Stalder G, Ruf T, Zahariev A, Blanc S, Giroud S. 2018. Implications of being born late in the active season for growth, fattening, torpor use, winter survival and fecundity. *Elife* 7:e31225.
- McAllan BM, Geiser F. 2014. Torpor during reproduction in mammals and birds: dealing with an energetic conundrum. *Integr Comp Biol* 54:516–32.
- McAllan BM, Geiser F. 2018. Torpor during reproduction in mammals and birds: Balancing energy expenditure for survival. Second Edi. ed, *Encyclopedia of Reproduction* Elsevier.

- McGuire LP, Leys R, Webber QMR, Clerc J. 2023. Heterothermic migration strategies in flying vertebrates. *Integr Comp Biol*.
- McKechnie AE, Freeman MT, Brigham RM. 2023. Avian heterothermy: A review of patterns and processes. *Integr Comp Biol* 0:1–11.
- McKechnie AE, Lovegrove BG. 2002. Avian facultative hypothermic responses: A review. *Condor* 104:705–24.
- McKechnie AE, Mzilikazi N. 2011. Heterothermy in afrotropical mammals and birds: A review. *Integr Comp Biol* 51:349–63.
- Mzilikazi N, Lovegrove BG. 2002. Reproductive activity influences thermoregulation and torpor in pouched mice, *Saccostomus campestris*. *J Comp Physiol B Biochem Syst Environ Physiol* 172:7–16.
- Nowack J, Cooper CE, Geiser F. 2016. Cool echidnas survive the fire. *Proc R Soc B Biol Sci* 283:20160382.
- Nowack J, Dausmann KH. 2015. Can heterothermy facilitate the colonization of new habitats? *Mamm Rev* 45:117–27.
- Nowack J, Levesque DL, Reher S, Dausmann KH. 2020. Variable climates lead to varying phenotypes: “weird” mammalian torpor and lessons from non-holarctic species. *Front Ecol Evol* 8:60.
- Nowack J, Mzilikazi N, Dausmann KH. 2023. Saving energy via short and shallow torpor bouts. *J Therm Biol* 114:103572.
- Nowack J, Rojas AD, Körtner G, Geiser F. 2015. Snoozing through the storm: torpor use during a natural disaster. *Sci Reports* 2015 5:1–6.
- Nowack J, Stawski C, Geiser F. 2017. More functions of torpor and their roles in a changing world. *J Comp Physiol B* 2017 1875 187:889–97.
- Nowack J, Stawski C, Geiser F, Levesque DL. 2023. Rare and opportunistic use of torpor in mammals – an echo from the past? *Integr Comp Biol*.
- Nowack J, Tarmann I, Hoelzl F, Smith S, Giroud S, Ruf T. 2019. Always a price to pay: Hibernation

- at low temperatures comes with a trade-off between energy savings and telomere damage. Biol Lett 15:20190466.
- O'Mara MT, Rikker S, Wikelski M, Maat A Ter, Pollock HS, Dechmann DKN. 2018. Heart rate reveals torpor at high body temperatures in lowland tropical free-tailed bats. R Soc Open Sci 4:171359.
- O'Mara MT, Wikelski M, Voigt CC, Maat A Ter, Pollock HS, Burness G, Desantis LM, Dechmann DKN. 2017. Cyclic bouts of extreme bradycardia counteract the high metabolism of frugivorous bats. Elife 6:1–20.
- Palchykova S, Crestani F, Meerlo P, Tobler I. 2006. Sleep deprivation and daily torpor impair object recognition in Djungarian hamsters. Physiol Behav 87:144–53.
- Palchykova S, Deboer T, Tobler I. 2002. Selective sleep deprivation after daily torpor in the Djungarian hamster. J Sleep Res 11:313–19.
- Powers DR, Brown AR, Van Hook JA. 2003. Influence of normal daytime fat deposition on laboratory measurements of torpor use in territorial versus nonterritorial hummingbirds. Physiol Biochem Zool 76:389–97.
- Price ER, Dzialowski EM. 2018. Development of endothermy in birds: patterns and mechanisms. J Comp Physiol B 188:373–91.
- Reher S, Dausmann KH. 2021. Tropical bats counter heat by combining torpor with adaptive hyperthermia. Proc R Soc B Biol Sci 288:20202059.
- Reher S, Ehlers J, Rabarison H, Dausmann KH. 2018. Short and hyperthermic torpor responses in the Malagasy bat *Macronycteris commersoni* reveal a broader hypometabolic scope in heterotherms. J Comp Physiol B 188:1015–27.
- Rossi GS, Welch KC. 2023. Leptin resistance does not facilitate migratory fattening in Ruby-throated hummingbirds (*Archilochus colubris*). Integr Comp Biol 0:1–12.
- Ruf T, Geiser F. 2015. Daily torpor and hibernation in birds and mammals. Biol Rev 90:891–926.
- Schwartz C, Hampton M, Andrews MT. 2013. Seasonal and regional differences in gene expression in the brain of a hibernating mammal. PLoS One 8:e58427.

- Shankar A, Cisneros INH, Thompson S, Graham CH, Powers DR. 2022. A heterothermic spectrum in hummingbirds. *J Exp Biol* 225:jeb243208.
- Shankar A, Schroeder RJ, Wethington SM, Graham CH, Powers DR. 2020. Hummingbird torpor in context: duration, more than temperature, is the key to nighttime energy savings. *J Avian Biol* 51:jav.02305.
- Smith WK, Roberts SW, Miller PC. 1974. Calculating the nocturnal energy expenditure of an incubating Anna's hummingbird. *Condor* 76:176–83.
- Song X, Körtner G, Geiser F. 1997. Thermal relations of metabolic rate reduction in a hibernating marsupial. *Am J Physiol Integr Comp Physiol* 273:R2097–2104.
- Staples JF. 2016. Metabolic flexibility: hibernation, torpor, and estivation. In: *Comprehensive Physiology* Hoboken, NJ, USA: John Wiley & Sons, Inc. p. 737–71.
- Stawski C, Geiser F. 2010. Fat and fed: frequent use of summer torpor in a subtropical bat. *Naturwissenschaften* 97:29–35.
- Stawski C, Körtner G, Nowack J, Geiser F. 2015. The importance of mammalian torpor for survival in a post-fire landscape. *Biol Lett* 11:20150134.
- Tessier SN, Wu C-W, Storey KB. 2019. Molecular control of protein synthesis, glucose metabolism, and apoptosis in the brain of hibernating thirteen-lined ground squirrels. *Biochem Cell Biol* 97:536–44.
- Tucker VA. 1966. Diurnal torpor and its relation to food consumption and weight changes in the California pocket mouse *Perognathus californicus*. *Ecology* 47:245–52.
- Turbill C, Smith S, Deimel C, Ruf T. 2012. Daily torpor is associated with telomere length change over winter in Djungarian hamsters. *Biol Lett* 8:304–7.
- Viblanc VA, Criscuolo F, Sosa S, Schull Q, Boonstra R, Saraux C, Lejeune M, Roth JD, Uhlrich P, Zahn S, Dobson FS. 2022. Telomere dynamics in female Columbian ground squirrels: recovery after emergence and loss after reproduction. *Oecologia* 199:301–12.
- Wacker CB, McAllan BM, Körtner G, Geiser F. 2017. The role of basking in the development of endothermy and torpor in a marsupial. *J Comp Physiol B* 187:1029–38.

- Walker JM, Garber A, Berger RJ, Heller HC. 1979. Sleep and estivation (shallow torpor): continuous processes of energy conservation. *Science* (80-) 204:1098–1100.
- Walker JM, Glotzbach SF, Berger RJ, Heller HC. 1977. Sleep and hibernation in ground squirrels (*Citellus* spp): electrophysiological observations. *Am J Physiol Integr Comp Physiol* 233:R213–21.
- Williams CT, Goropashnaya A V., Buck CL, Fedorov VB, Kohl F, Lee TN, Barnes BM. 2011. Hibernating above the permafrost: Effects of ambient temperature and season on expression of metabolic genes in liver and brown adipose tissue of arctic ground squirrels. *J Exp Biol* 214:1300–1306.
- Wilson R, Shepard E, Liebsch N. 2008. Prying into the intimate details of animal lives: use of a daily diary on animals. *Endanger Species Res* 4:123–37.
- Wojciechowski MS, Pinshow B. 2009. Heterothermy in small, migrating passerine birds during stopover: use of hypothermia at rest accelerates fuel accumulation. *J Exp Biol* 212:3068–75.
- Zenzal TJ, Moore FR. 2016. Stopover biology of Ruby-throated Hummingbirds (*Archilochus colubris*) during autumn migration. *Auk* 133:237–50.
- Zervanos SM, Salsbury CM. 2003. Seasonal body temperature fluctuations and energetic strategies in free-ranging eastern woodchucks (*Marmota monax*). *J Mammal* 84:299–310.