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Doctoral thesis

Mari Aas Fjelldal

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Thesis for the degree of
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Trondheim, March 2023

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Brunlangøre
Brown long-eared bat
Plecotus auritus

Bredøre
Western barbastelle
Barbastella barbastellus

Sørflaggermus
Southern bat
Eptesicus serotinus

Nordflaggermus
Northern bat
Eptesicus nilssonii

Dvergflaggermus
Soprano pipistrelle
Pipistrellus pygmaeus

Trollflaggermus
Nathusius's pipistrelle
Pipistrellus nathusii

Tusseflaggermus
Common pipistrelle
Pipistrellus pipistrellus

Skjeggflaggermus
Whiskered myotis
Myotis mystacinus

Børsteflaggermus
Natterer's bat
Myotis nattereri

Storflaggermus
Noctule bat
Nyctalus noctula

Vannflaggermus
Daubenton's bat
Myotis daubentonii

Skimmelflaggermus
Particoloured bat
Vespertilio murinus

Skogflaggermus
Brandt's bat
Myotis brandtii

The bats of Norway. Illustrations by Mia Aas Fjelldal.

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Abstract

A majority of bat species are small, insectivorous and strictly nocturnal. With temporally restricted foraging opportunities, a food source that varies with weather fluctuations, and high energetic costs of powered flight and thermoregulation, many bat species rely upon the efficient energy saving state of 'torpor' to avoid mismatches to their energy budgets. However, various costs associated with torpor expressions create trade-offs that likely result in adaptive variation in the strategic use of heterothermic responses across species and individuals. With this thesis, I aimed to identify and explore the effect and magnitude of various environmental and individual state conditions on strategic torpor expressions in small bats during summer.

At high latitudes summer nights are short and light, which put further constraints on the time bats have available to forage. To investigate how high-latitude living bats cope with the challenging summer conditions and how climate change might impact northern geographical distribution ranges, I collected skin temperature data from three bat species in Norway. To fully understand how environmental effects and individual state impacted activity patterns and torpor use, I decomposed within- and among-subject effects after fitting mixed effect models to the data. I conducted similar analyses on an extensive dataset previously collected on Australian eastern long-eared bats (*Nyctophilus bifax*), to compare how insectivorous bats that inhabit vastly different climate zones alter their torpor expressions in response to local environmental conditions. Finally, to properly investigate how current energetic reserves may impact immediate and future strategic decisions in various scenarios, I developed a state-dependent optimisation model to test how bats facing short summer nights at high latitudes optimise individual decisions across the daily cycle. The studied bats expressed various responses to different weather variables but were all highly impacted by temperature conditions both across and within species, latitudes and climate zones. They showed various degrees of state-dependency, this being body mass or reproductive state, in their responses to current weather or light conditions. State-dependency for non-reproductive bats was fully explored in the theoretical model framework of optimal decisions, and I discovered that individual state may be a strong driver of current and future strategic decisions, but that the strength of such state-dependencies vary with temperature- and light-scenarios.

Overall, the results highlight the resilience bats may have to apparent challenges, such as limited foraging time, fluctuating food availability and periodically unfavourable weather patterns at high latitudes. However, it also demonstrates the importance and complexity of weather condition effects on the management of individual energy budgets, implying that the ongoing environmental change may strongly impact torpor patterns across seasons and populations, although light-conditions at high latitudes appear to be a restricting factor for expanding northern distribution ranges.

List of Papers

Paper I

Fjelldal, M.A., Wright, J., & Stawski, C. (2021). Nightly torpor use in response to weather conditions and individual state in an insectivorous bat. Oecologia, 197(1), 129-142.

Paper II

Fjelldal, M.A., Sørås, R., & Stawski, C. (2022). Universality of Torpor Expression in Bats. Physiological and Biochemical Zoology, 95(4), 326-339.

Paper III

Fjelldal, M.A., Stawski, C., Sørås R., & Wright, J. (2022) Determining the different phases of torpor from skin- or body temperature data in heterotherms. Journal of Thermal Biology, 103396.

Paper IV

Fjelldal, M. A., Muller, A. S., Ratikainen I. I., Stawski, C., & Wright, J. The small-bat-in-summer paradigm: energetics and adaptive behavioural routines of bats investigated through a stochastic dynamic model. Submitted manuscript.

Paper V

Fjelldal, M.A., Wright, J., Sørås R., & Stawski, C. Physiological and behavioural strategies of brown long-eared bats in summer at high latitudes: torpor, foraging times and effects of reproductive condition. Manuscript.

Paper I: CS and JW designed the study; CS conducted the fieldwork and collected the data; MAF performed analyses and interpretation with input from CS and JW; MAF led the writing of the manuscript, which was commented on and revised by CS and JW. **Paper II**: CS and MAF conceived the study; MAF and RS conducted fieldwork, and all authors contributed to the collection of published data from the literature; MAF carried out the data analyses; MAF wrote the manuscript with input from CS and RS. **Paper III**: JW, MAF and CS conceived the study; RS and MAF conducted fieldwork and collected data; MAF developed the methodology with significant contribution from JW; MAF led the writing of the manuscript with input from all co-authors. **Paper IV**: JW and CS designed the study; ASM, IIR and MAF developed the theoretical framework and created the r-codes for the models; MAF performed analyses and interpretation with input from all co-authors; MAF led the writing of the manuscript with input from all co-authors. **Paper V**: CS, JW and MAF designed the study; MAF and RS conducted the fieldwork and collected the data; MAF performed the analyses with input from CS and JW; MAF wrote the manuscript with input from all co-authors.

Papers not included in this thesis

Skåra, K.H., Bech, C., **Fjelldal, M.A.**, van Der Kooij, J., Sørås, R., & Stawski, C. (2021). Energetics of whiskered bats in comparison to other bats of the family Vespertilionidae. Biology Open, 10(8), bio058640.

Sørås, R., **Fjelldal, M.A.**, Bech, C., van der Kooij, J., Skåra, K.H., Eldegard, K., & Stawski, C. (2022). State dependence of arousal from torpor in brown long-eared bats (*Plecotus auritus*). Journal of Comparative Physiology B, 192(6), 815-827.

Contents

1. Introduction

1.1. The challenges faced by small endotherms in seasonal environments

The primary life goal of animals is to contribute to the next generation, and to do so they must grow and successfully reproduce, for which they need sufficient energy (Caswell 1989; Stearns 1992). However, in the wild animals are constantly at risk of not meeting their energy requirements, which is compounded by both predictable and unpredictable changes to the environment (e.g. diurnal/seasonal effects and weather, respectively). Furthermore, many animals face exposure to predators during their foraging activities, consequently resulting in individual optimal foraging decisions being highly dependent upon current prospects of acquiring sufficient food, the risk of being predated upon, and the immediate and long-term risk of starvation (Houston & McNamara 1999; Stephens *et al.* 2007; Krebs & Davies 2009).

In order to predict an animal's scope for survival and reproduction in a given environment, we need to understand the drivers and consequences of individual decision-making, which involves the management of physiological processes along with ecological and environmental factors, foraging strategies and predation threat. For small endotherms living in seasonal environments, particular challenges must be overcome if they are to meet their energy requirements, survive and successfully produce viable offspring to continue their gene-contribution to future generations.

1.1.1. Cost of thermoregulation

Endothermy is a remarkable adaptation in vertebrates. The evolved ability for metabolic heat production allows endotherms to keep their body temperature (T_b) high and stable across a wide range of thermal environments, which has largely improved their scope for activity, growth and expansion of species distributions (Bennett & Ruben 1979; Clarke & Pörtner 2010). However, the energetic maintenance cost of the high metabolism required to sustain a high and stable T_b results in substantial energetic demands, which the endotherms must meet through additional and constant food consumption.

Although large-bodied endotherms naturally have higher absolute metabolic rates (MR) than small-bodied endotherms (Fig. 1a), the mass-specific MR is considerably greater for smaller species compared with larger species (Fig. 1b). This is generally explained by the scaling relationship between body mass and surface area, with smaller animals having larger surface area to volume ratios (Sarrus & Rameaux 1838; White & Kearney 2011). Because heat is

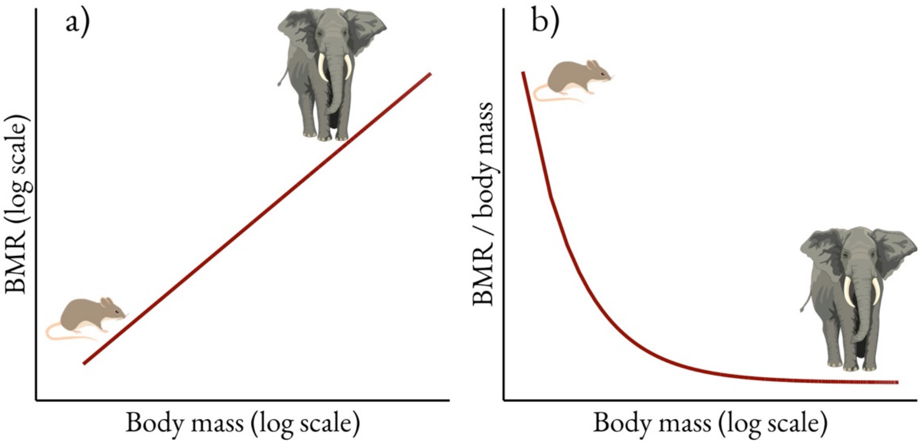

Figure 1: Simplistic graphs showing the relationships between body mass and basal metabolic rate (BMR) in endothermic species. **a)** The positive linear relationship between body size and absolute measures of BMR. **b)** The curvilinear negative allometric relationship between body mass and mass specific BMR across endotherms, where the power function explaining this relationship is described as aM^b, a signifying a scaling constant, M being the body mass of the animal, and b representing the scaling exponent.

actively lost across the body surface area whenever the outer thermal environment is colder than the T_b, smaller animals with larger surface area to volume ratios must generate more metabolic heat to compensate for the higher heat loss, commonly known as the 'surface-law' (Rubner 1883). Small endotherms therefore have high metabolic costs per unit body mass, and consequently need a greater mass-specific food consumption to meet their daily energy requirements of bodily maintenance.

The energetics that animals must balance with their foraging activities further depends upon the thermal environment that they experience. Although most endotherms have fur, fat or feathers that provide insulation, body heat is inevitably lost to the environment at increasing rates as the environment gets colder, resulting in increased rates of metabolic heat production if an endotherm is to maintain its high and stable T_b (Withers *et al.* 2016). These adaptive changes in MR across a range of temperature values are commonly expressed using a thermoregulatory curve, as shown in Fig. 2. Within a certain range of environmental temperatures, known as the thermoneutral zone (TNZ), the animal can maintain its heat balance without regulating the metabolic heat production or its evaporative heat loss, and thus only expresses basal metabolic rate (BMR) within this zone (Bligh & Johnson 1973). Above the TNZ, an endotherm must increase its evaporative heat loss to avoid overheating, while below it the endotherm must increase metabolic heat production through shivering and non-shivering thermogenesis in order to maintain its T_b (Bligh & Johnson 1973; Hohtola 2004; Withers *et al.* 2016).

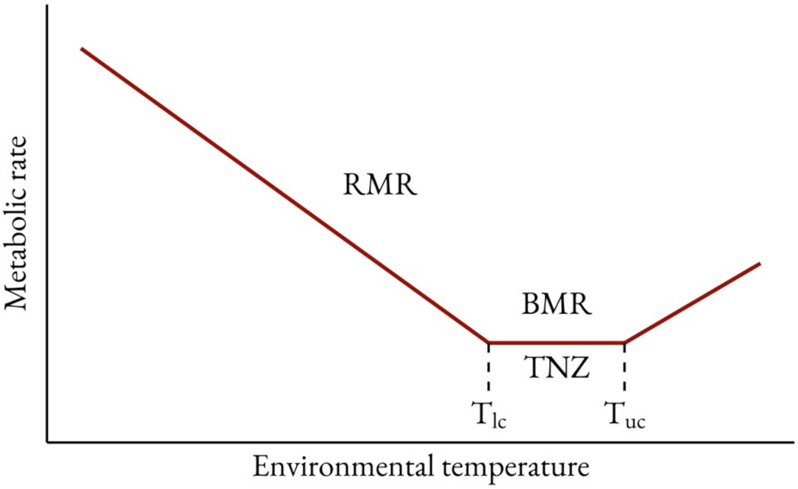

Figure 2: Simplistic illustration of a general endothermic thermoregulatory curve. Within the temperature range of the thermoneutral zone (TNZ) an animal expresses its minimum metabolic rate (MR) for maintaining bodily processes, known as the basal metabolic rate (BMR). The upper and lower critical temperature (T_{uc} and T_{lc}, respectively) indicate the limits of the TNZ. Above and below these limits, the MR increases linearly with the greater physiological processes needed to maintain suitable and stable body temperatures. This is known as the resting metabolic rate (RMR) and is dependent upon the environmental temperature that the animal is experiencing.

1.1.2. Living in a seasonal environment

All organisms live in more or less seasonal environments and therefore face temporal changes to their climate throughout the yearly cycle (Fretwell 1972). Increasing latitudes are associated with stronger seasonalities, where predictable but substantial changes to climatic conditions and, consequently, resource availabilities often leads to seasonal migration evolving as an adaptive strategy in many species (Ramenofsky & Wingfield 2007). However, for species that do not migrate, seasonal changes can impose large energetic demands that the residents must cope with in order to survive. For diurnal endotherms facing the long and cold winters at high latitudes, these demands arise from increased thermoregulatory costs increasing overall daily energetic requirements, and from decreases in food availability and the number of daylight hours they are able to spend foraging (see McNamara *et al.* 1994).

A well-known example from both the theoretical and the empirical literature that explores this apparent energetic dilemma is the ‘small-bird-in-winter’ paradigm (Lehikoinen 1987; Bednekoff & Houston 1994; McNamara *et al.* 1994; Brodin 2007). Although small birds can put on fat reserves to help them survive the winter, they can only carry enough fat reserves to survive for a day or two without foraging (King 1972; Lehikoinen 1987). To survive a full winter, small birds must therefore spend a considerable part of each winter day actively searching for food, although by doing so they increase their risk of exposure to predators (McNamara & Houston 1990). The chances of predation further increase with energy storage as heavier birds are less agile and thus less successful in escaping attacks from aerial and terrestrial predators (see Lima 1986; McNamara & Houston 1990; Brodin 2007). With both the risk of starvation and the risk of predation being dependent upon individual levels of energy reserves, or 'state', the optimum foraging and fat storage strategy can be calculated as a diurnal/seasonal series of state-dependent decisions, which has been explored in various stochastic dynamic models such as the 'small bird in winter' (reviewed by Brodin 2007). State-dependent decision-making has been extensively explored across different environmental scenarios, and has substantially contributed to our understanding of individual adaptive strategies and persistence in challenging and/or stochastic environments (Brodin 2007).

However, it is not only the winter at high latitudes that poses energetic challenges for small animals. In seasonal environments, spring and summer are for many species the critical time of year when resource abundance and warmer thermal environments allow individuals to extend energetic investment from not only surviving but also to reproducing (Fretwell 1972). Because energetic resources will always be a limiting factor when investing in various life-history traits such as growth, longevity and fecundity (Stearns 1992), strategic decisions regarding energy allocation for self-maintenance versus reproductive effort are also crucially dependent upon individual state (McNamara & Houston 1996). State-dependent energetic trade-offs are therefore present in different forms throughout all different seasons for small animals inhabiting high-latitude environments. Maximizing fitness through survival and/or reproduction is thus closely linked to the individual management of energy reserves and strategic decisions that optimize both current and future fitness prospects.

1.2. Heterothermy

Because endothermy is so energetically expensive and can be a contributing cause to energetic mismatches during periods of food shortage, a range of endothermic species have developed strategies to temporarily abandon strict thermal homeostasis in order to save energy (or for other benefits; see section 1.2.1.). In cold conditions, lowering T_b can be energetically favourable for two reasons: (i) it reduces heat loss to the environment; and (ii) it decreases energy requirements in the tissues (Withers *et al.* 2016). In warm or arid conditions, although T_b may not decrease once thermal homeostasis is lost, animals can also temporarily abandon active metabolic thermoregulation and other physiological processes to save energy and, perhaps more importantly, water (Wilz & Heldmaier 2000; Storey 2002; Reher & Dausmann 2021). Heterothermic strategies therefore exist in various environments across taxa, although strategies for coping with the cold are perhaps most frequently reported (Geiser & Brigham 2012; Nowack *et al.* 2017). In birds, facultative hypothermia is a widespread strategy for dealing with cold conditions, where individuals can reduce their T_b by up to several degrees during the resting phase at night to obtain large energetic savings (McKechnie & Lovegrove 2002). However, relative energy savings may be reduced at very low temperatures, because hypothermic birds still need to regulate their T_b through thermogenesis to avoid freezing (e.g. Reinertsen & Haftorn 1986).

A much more efficient energy-saving strategy found in endotherms is 'torpor'. Species capable of employing torpor are commonly referred to as 'heterothermic endotherms' or simply 'heterotherms', because they are able to readily switch between maintaining a high euthermic T_b by thermoregulating versus allowing T_b to track ambient temperatures by thermoconforming (Geiser & Ruf 1995). Torpor expressions are commonly categorised into two main types: daily torpor expressed by daily heterotherms and multiday torpor bouts expressed by hibernators (Lyman *et al.* 1982; Currie *et al.* 2022). The onset of these heterothermic responses is generally triggered by environmental cues (e.g. food or water shortage, low ambient temperatures, photoperiod), upon which the heterotherm activates a cyclic parasympathetic response which results in induced skipped heartbeats, regular asystoles and a general deceleration of even heart beats (Milsom *et al.* 1999). Reduced heart rate and respiration further leads to less oxygen being distributed to the tissues, thus reducing the MR, further resulting in less heat being produced as a by-product. As the T_b of the animal starts to fall, heart rate and MR are further reduced until the parasympathetic influence is gradually withdrawn and a balance is obtained between parasympathetic and sympathetic dominance (Milsom *et al.* 1999). As such, facultative heterothermy is generally associated with substantial and reversible reductions in heart rate, MR and T_b, although recent research describing expressions of 'hot' torpor (e.g. Reher *et al.* 2018) has shown that the latter characteristic is not necessarily observed if the ambient temperature is high and stable.

1.2.1. Benefits

Species employing daily torpor and/or hibernation can be found across a wide range of taxa in birds and mammals, but they are generally small bodied, although there are exceptions (e.g. badgers and bears) (Geiser 1998; Ruf & Geiser 2015). The wide taxonomic distribution of heterothermy indicates that these strategies are highly beneficial to individual survival across environments and life histories, and that in the long-term they facilitate species persistence (Geiser & Turbill 2009; Liow *et al.* 2009; Stawski *et al.* 2014).

The most frequently reported benefit of employing torpor and hibernation is the substantial energy savings animals can achieve when their environment is cold and food scarce, such as during winter (Lyman *et al.* 1982). Deep torpor metabolic rates are usually less than 3% of those measured during euthermic levels at the same environmental temperatures, resulting in substantial reductions of energy requirements (Geiser 1988; Heldmaier & Ruf 1992). However, earlier assumptions concerning torpor and hibernation being used only as a winter survival strategy has been challenged in recent years (Heldmaier *et al.* 2004; Geiser & Brigham 2012; Stawski *et al.* 2014; Nowack *et al.* 2017). Other identified advantages of torpor and hibernation now include improved fat storage during migration, prolonged sperm storage, delayed parturition until environmental conditions improve, improved persistence to droughts or natural disasters such as storms or fires, reduced parasite loads, and reduced exposure to predators (Geiser & Brigham 2012; Nowack *et al.* 2017).

Regardless of the causation triggering the heterothermic response, daily torpor and hibernation can often represent the most effective energy-saving strategies available to endotherms (Heldmaier *et al.* 2004), which is likely why these strategies have been linked to lower species extinction rates (Geiser & Turbill 2009; Liow *et al.* 2009).

1.2.2. Costs

Despite the extensive energetic (and other) advantages of employing torpor and hibernation, certain costs are associated with heterothermic responses, which can lead to strategic trade-offs. During hibernation, animals risk physiological costs of metabolic depression, such as tissue damage, oxidative stress, immunodeficiency, DNA damage, sleep deprivation, cognitive defects and digestive malfunction (Humphries *et al.* 2003; Landes *et al.* 2020). It has therefore been suggested that hibernating animals need to periodically arouse to reverse the detrimental physiological consequences of metabolic depression (Humphries *et al.* 2003). However, arousing from torpor may in itself pose large energetic and physiological costs to an individual, particularly when rewarming from low temperatures (Currie *et al.* 2015), and in general accounts for the majority of over-winter energy expenditure whilst hibernating (Thomas *et al.* 1990; Dunbar & Tomasi 2006; Karpovich *et al.* 2009).

Torpor bouts outside of the hibernation season may also have serious detrimental effects. For reproductive individuals, torpor use can slow foetal development (Racey & Swift 1981), halt milk production (Wilde *et al.* 1999), or negatively impact spermatogenesis (Gagnon *et al.* 2020). Torpor and reproduction have therefore previously been considered as incompatible (Wimsatt 1969), but torpor use throughout the reproductive cycle is today commonly reported across heterothermic species, although such torpor expressions may differ from those found in non-reproductive conspecifics (Geiser 2021) (see section 1.2.3.).

Both long and short torpor bouts are further associated with ecological costs, such as the cost of missed foraging opportunities (e.g. Levy *et al.* 2012), decreased mobility leading to reduced ability to escape predators (Humphries *et al.* 2003; Carr & Lima 2013; Haarsma & Kaal 2016), and loss of potential mating opportunities (e.g. Thomas *et al.* 1979). The various potential physiological and ecological costs associated with heterothermic responses therefore suggests a cost-benefit approach when predicting the optimal timing and levels of torpor and hibernation (Humphries *et al.* 2003; Boyles *et al.* 2020; Landes *et al.* 2020). However, individual energetic state is also expected to play an important role in such predictions.

1.2.3. State-dependency

The magnitude of the trade-offs between prospective benefits and potential associated costs of employing torpor will be highly dependent upon the species and the environmental challenges that they face. However, variation in individual state has been identified as a critical cause of observed variability in the expression of heterothermic responses. For example, reproductive state is a strong driver of torpor expressions across taxa, where pregnant or lactating females and reproductive males have been found to express less and/or shallower torpor bouts to avoid detrimental effects to foetal development, milk production or spermatogenesis (reviewed in Geiser 2021). At high latitudes with short reproductive seasons, a slowing of foetal development or offspring growth could be very costly given that both the mother and offspring will have less time to prepare for the upcoming winter season.

Individuals that are not in their reproductive cycle have also been found to show substantial variation in heterothermic responses, likely due to individual-level state-dependent trade-offs. Because of the various physiological and ecological costs involved, torpor and hibernation are expected to be reduced in individuals that can afford to avoid heterothermy. For example, torpor bouts during hibernation in chipmunks were observed to be shorter and shallower if individuals had energy reserves available (French 2000; Munro *et al.* 2005; Landry-Cuerrier *et al.* 2008). Furthermore, larger bats (*Myotis lucifugus*) prefer warmer microclimates within the hibernacula compared to lighter conspecifics (Boyles *et al.* 2007), while individuals with greater energy reserves spend relatively less time torpid in several species of heterotherms (Wojciechowski *et al.* 2007; Bieber *et al.* 2014; Zervanos *et al.* 2014; Sørås *et al.* 2022).

Individual energetic state is therefore likely to be important in decision-making regarding heterothermy in most heterotherms, although critical measures such as levels of fat storage are rarely reported. Such state-dependency is also predicted to interact with environmental conditions and with species-specific cost-benefit ratios of expressing torpor and hibernation, providing quite specific quantitative hypotheses that demand exploration.

1.2.4. Quantifying torpor

Quantifying individual heterothermic responses in a lab environment can be achieved using various methods, such as measurements of oxygen consumption, carbon dioxide production, or monitoring of heart rate. However, quantifying torpor in small heterotherms in their natural environments can be more challenging, given that certain methods may require surgery, advanced technical equipment and/or a recapture of the animal (see McCafferty *et al.* 2015). Nevertheless, quantifying torpor and hibernation in free-ranging heterotherms is of great importance if we are to understand the natural use, causation and consequences of such strategic energetic responses.

The T_b of a heterotherm typically decreases when entering torpor, unless the animal is in a very warm thermal environment (e.g. Reher & Dausmann 2021). Therefore, one method that is frequently used to assess T_b and thus instances of torpor in field studies on small-bodied animals is the measurement of skin temperatures (T_{skin}) using external temperature-sensitive transmitters (Barclay *et al.* 1996; McCafferty *et al.* 2015). T_{skin} has been found to predictably covary with T_b across thermal environments whenever the animal is resting or torpid (Audet & Thomas 1996; Barclay *et al.* 1996; Dausmann 2005), although it can be quite inaccurate when the animal is active (Willis & Brigham 2003). Because this method is less invasive than surgical implantations and does not necessarily require the recapture of the animal, it has become a popular way to collect individual data on torpor in free-ranging heterotherms.

When collecting T_{skin} (or T_b) data in the field without corresponding information on oxygen consumption or heart rate, it is common to identify torpor bouts using temperature threshold values, assigning values below a specified critical temperature as 'torpor' and values above it as 'euthermic'. However, deciding upon the best way to determine such threshold values has proven challenging and has led to an extensive methodological discussion in the scientific literature (Barclay *et al.* 2001; Willis & Brigham 2003; Willis 2007; Boyles *et al.* 2011a; Brigham *et al.* 2011; Canale *et al.* 2012). Furthermore, strict threshold values overlook or conflate the periods of time needed to enter into and arouse from full torpor, such that any torpor bouts necessarily consist of a 'cooling' phase, a 'stable' phase and a 'rewarming' phase.

One method capable of also identifying such cooling and rewarming phases in torpor bouts from temperature data alone in heterotherms is nonstationary waveform analysis (Refinetti

2004; Levesque *et al.* 2017). Unfortunately, nonstationary waveform analysis becomes rather inaccurate whenever the run of data includes missing observations (D. Levesque, personal communication, September 15th 2022), which is common in many of these field datasets. An alternative method for quantifying heterothermic responses, and which also allows for better cross-species comparisons, is the heterothermy index (HI) developed by Boyles *et al.* (2011b). By using all T_{skin} (or T_b) data recordings of an individual or population, this method can evaluate the level of heterothermy expressed by homeotherms and heterotherms alike. However, because HI does not strictly differentiate between torpor and non-torpor (which is one of its advantages), it is not intended as a tool for investigating individual torpor use strategies within populations (Boyles 2019). In addition, as noted earlier, fluctuations in T_{skin} recorded during euthermia could be caused by individual activity and/or external thermal influences, as opposed to just the active regulation of thermogenesis. Therefore, using the HI to evaluate levels of heterothermy in populations and/or individuals may be less accurate in studies that utilise external T_{skin} transmitters, depending upon the particular study system or species involved.

As a result, the use of a simple threshold T_{skin} (or T_b) value remains the most commonly applied field method to determine torpor expressions in heterotherms. There is therefore room for improvement in existing methodologies to more accurately quantify torpor bouts and their different phases from T_{skin} (or T_b) data alone using field-derived temperature data on free-ranging individuals.

1.3. Heterothermy within the order of Chiroptera (bats)

Bats belong to a mammalian order (Chiroptera) where torpor use is particularly widespread among species (Stawski *et al.* 2014). The order of Chiroptera, with its ~1400 species, contains more than 20% of all described mammal species found on Earth, making it the second largest mammalian order after rodents in terms of species richness (Zachos 2020). Bats are found on all continents except Antarctica and can be extremely diverse in their ecology, morphology and physiology across species (Fig. 3; Kunz & Fenton 2005). Still, a majority of bat species are small bodied, insectivorous and strictly nocturnal (Simmons & Conway 2005). As such, they face potentially high energetic costs of thermoregulation due to their large surface area to volume ratio and highly vascularized flight membranes that facilitate heat loss to the environment (Reeder & Cowles 1951). Furthermore, bats have extensive energetic costs associated with flight and echolocation (Kurta *et al.* 1989; Winter & Von Helversen 1998; Currie *et al.* 2020). Consequently, as they are temporally restricted in their foraging given their nocturnal lifestyle and prey on a food source that vary with environmental conditions like temperature and precipitation (see Taylor 1963; Speakman *et al.* 2000), insectivorous bats risk mismatches between their energy requirements and the energy gained during foraging flights. During inclement conditions, when energy costs are high and foraging benefits low, bats readily enter torpor to save energy in order to maintain a positive budget, particularly during the daytime when they would otherwise be resting and largely immobile in their day roosts. However, at night bats need to continuously balance the demand for energy acquisition via foraging with the benefits of saving energy through torpor, which presents them with different cost-benefit ratios than those they face during daytime.

Insect abundance is generally greater during the warmer daytime than at night, and it has therefore been questioned why insectivorous bats do not conduct their foraging flights to coincide with the higher food availability during the day instead of during the night (Speakman 1991b). Two of the main theories attempting to explain the nocturnal lifestyle of insectivorous bats are interspecific competition costs from insectivorous birds and the risk of predation from avian raptors such as hawks or falcons during daylight hours (Speakman 1991b; Speakman 1991a; Rydell & Speakman 1995; Speakman *et al.* 2000; Lima & O'Keefe 2013). Although direct observations of predation attacks on foraging bats are relatively rare (apart from attacks by hawks and falcons on large bat population emergences; Lima & O'Keefe 2013), predation threat remains perhaps the strongest supported theory as to why bats do not forage more frequently in daylight (Speakman 1991b). Predation threat is therefore expected to be an important factor in the decision of whether to forage or not in bats, which explains light sensitivity in bat species in environments where diurnal avian

Figure 3: Examples of different bat species to illustrate the considerable species diversity within the order of Chiroptera. Pictures were obtained through Unsplash.com and Pexels.com.

raptors (or other potential bat predators) are likely to be present (Lima & O'Keefe 2013; Saldaña-Vázquez & Munguía-Rosas 2013).

At high latitudes in the Northern hemisphere insectivorous bats face particular challenges to managing their energy budget. In addition to long and cold food-depleted winters, during which the bats need to hibernate in order to survive, summer seasons are not only short, but generally mild and can be periodically colder and rainy. Furthermore, the summer at high latitudes is associated with a photoperiod that leads to short light nights during midsummer, and this can dramatically restrict available foraging time for nocturnal creatures. The further north you go, the shorter and brighter the summer nights become, until there is a lack of 'true' night where the midnight sun does not set below the horizon. Despite these apparently unfavourable conditions, bat species are found up to subarctic latitudes with breeding colonies of northern bats (*Eptesicus nilssonii*) found even up above the Arctic circle (Rydell *et al.* 1994).

Bats in Norway therefore face the challenges of a short active season, during which they must successfully reproduce and raise their young before fattening up for the subsequent hibernation season. However, the restricted foraging time at night and variable weather conditions during a period of high energetic requirements makes the 'small bat in summer' into a challenge closely resembling that of the 'small-bird-in-winter' paradigm described earlier. Adaptively balancing torpor use and foraging activity should therefore be key to promoting the survival of small bats at high latitudes, allowing them to maintain a positive energy balance in the face of changing environmental conditions and reducing the risk of extinction in many species. Still, little is known about how high-latitudinal bats cope with the constant risk of an energetic mismatch and how they balance their strategic torpor use with any foraging requirements during light summer night conditions, or how energetic condition (i.e. fat reserves) or reproductive state influence individual decisions and over what time scales.

2. Aims and objectives

The central aim of this thesis was to investigate the relationships between torpor use and various environmental variables at the individual level on free-ranging bats, with an emphasis on high-latitude populations, in order to better understand their scope for persistence in a changing world.

I had four overarching questions, which I answered with five papers:

- Do environmental conditions that increase the thermal costs of nighttime resting, and/or decrease food availability and thus bat foraging benefits, result in changes in the nighttime use of torpor, and how does individual state affect such decisions?

  In **Paper I**, we investigated statistical effects of environmental conditions and individual body mass on nightly torpor use in Australian bats. In **Paper IV**, we developed a stochastic dynamic model framework to perform in-depth explorations of the effects of changing environmental conditions and individual energetic state on individual decisions in torpor use, foraging and resting. In **Paper V**, we quantified torpor characteristics and use across environmental conditions and reproductive states in a high-latitude living bat species in Norway.

- How do light conditions impact torpor use and nighttime activity levels in bats?

  In **Paper I**, we investigated the effect of moon illumination on nightly torpor use in Australian bats. In **Paper IV**, we used a stochastic dynamic model framework to compare torpor use across latitudes to investigate the effect of photoperiod. In **Paper V**, we explored the effect of lux levels and night length on torpor use, foraging and timing of emergence and return to the roost at night in Norwegian bats.

- Are torpor characteristics in bats similar across climate zones?

  In **Paper II**, we conducted a literature review to compare torpor characteristics, such as torpor metabolic rates and daily torpor patterns in bat populations across climate zones. In this, we used data from **Paper I** and **Paper V** as concrete examples to illustrate torpor expressions in bats from vastly different habitats.

- Can existing methods for determining torpor from T_{skin} data be improved?

  In **Paper III** we attempted to extend the threshold value method for not only identifying torpor, but to determine the different entry and arousal phases of a torpor bout from T_{skin} (or T_b) data in heterotherms.

3. Methods

3.1. Empirical data collection

For **Paper I** (and for part of **Paper II**), data had already been collected on eastern long-eared bats (*Nyctophilus bifax*) by Clare between 2007 and 2009 from one subtropical location (Iluka Nature Reserve) and one tropical location (Djiru National Park) in Australia (Fig. 4). A total of 26 bats were captured during the austral winter, spring and summer at the subtropical location, while 11 bats were captured during two consecutive winters at the tropical location.

In Norway, across three summer field seasons (2019-2021) I collected data from 39 brown long-eared bats (*Plecotus auritus*) in Nittedal, data from 11 northern bats (*E. nilssonii*) in Nittedal and Trondheim, and data from 10 Brandt's bats (*Myotis brandtii*) in Nittedal and close to Trondheim (Fig. 4) (used for part of **Paper II**, for **Paper III**, for part of **Paper IV**, and for **Paper V**). Unfortunately, the data collected from the Brandt's bats suffered from long periods of missing observations throughout the sample period for most of the individuals, likely because of tight roosting conditions that coiled the transmitter-antennas and disrupted the signals, while for the northern bats only two were caught in Nittedal, which made empirical

Figure 4: Field sites for the empirical data collection in Australia and Norway. The picture of the *N. bifax* is taken by Clare Stawski, while the pictures of the three Norwegian species are taken by Mari A. Fjelldal.

data comparisons between the two Norwegian sites challenging for these two species. However, data from the northern bats were used for comparisons of results generated from the theoretical model framework (**Paper IV**; see section 3.4).

During both the Australian and the Norwegian field work, bats were captured using mist nets and were subsequently tagged with heat-sensitive radio-transmitters by first removing a patch of fur from their dorsal region before attaching the tag with a skin adhesive. The bats were afterwards released at the capture site and tracked to their day roosts, where external data loggers were set up to record transmitter pulse frequencies every ten minutes. The frequencies could afterwards be converted to T_{skin} values as the transmitters had been calibrated in water baths with temperatures ranging between 5 to 40°C prior to attaching them to the bats. Data were collected until the transmitter was shed by the bat, usually within one week after attachment, although some kept their tags on for up to several weeks.

At each location, heat-sensitive data loggers were hung up outside of each day roost to monitor the air temperature, and at the Norwegian locations light-meters were placed out to record lux levels continuously across the field seasons. Meteorological data were obtained through webpages providing detailed recordings from weather stations in close proximity to the field sites.

3.2. Mixed models and within vs. among-subjects effects

To analyse our empirical data on torpor expressions in **Paper I** and **Paper V**, we constructed linear mixed-effect models with individual ID included as a random effect in all analyses. Mixed models can handle hierarchically structured data and account for non-independence in the observations (such as multiple recordings from the same individual) by modelling the structure of the covariance between observations introduced by the grouping within the data. Such models are therefore powerful tools for analysing data containing non-independent observations, particularly as random effects do not add degrees of freedom to the models. All continuous explanatory variables were variance scaled and centered to facilitate comparisons when determining the strongest predictors in each analysis. We then conducted model selections from global models to find the best-fit final model construction for the data.

When fitting a linear mixed model to investigate population-level effects from individual-level observations, the scaling and centering is normally done on the whole dataset and therefore does not account for the variation in environmental conditions faced by each individual. By chance, different individuals may have experienced very different environmental conditions during data collection, and thus not everyone will necessarily have been recorded responding to the same mean and variance in the environmental variables. There is therefore always the potential risk that any population-level responses are in reality caused by among-individual effects (hereafter referred to as 'among-subject effects') and that the individual responses are, in fact, not in accordance with the observed overall population level effect (see Fig. 1 in van de Pol and Wright (2009) for examples). A relatively simple solution to this issue was presented by van de Pol and Wright (2009): by scaling and centering continuous explanatory variables within each individual, mixed-effect models can be used to predict within-subject effects and verify whether the population level responses are mainly driven by within- or among-subjects effects in the data.

We therefore applied these methods to our identified best models for each analysis in **Paper I** and **Paper V** to ensure that all identified effects were in fact caused by individuals responding to their environment and were not results of the individuals having been measured across different environmental ranges during the data collection.

3.3. Quantifying torpor based on temperature differentials

In **Paper III**, we improved on the threshold method by determining the various phases of a torpor bout using a temperature differential method. This involved identifying torpor cooling 'entries', 'stable torpor' periods and rewarming 'arousal' phases from data showing the rate of change in T_{skin} from the previous measurement. Temperature differential models have previously been used to describe T_{skin} or T_b fluctuations (Utz *et al.* 2007; Gordon 2009), but these applications are either not suitable for describing torpor expressions or are aimed at lab-derived measurements where the thermal environment is regulated and closely monitored. We incorporated the differential method as a second step after initially identifying torpor bouts using a threshold approach to our data.

3.4. Dynamic state variable models

Theoretical model frameworks allow us to investigate the consequences of a range of relationships and scenarios that we would otherwise be unable to test. Dynamic state variable stochastic dynamic models are programming models that through the notions of constraints and trade-offs related to animal decisions and prospective fitness can calculate individual optimal decisions across time, environments and states (Mangel & Clark 1988; Clark & Mangel 2000). Dynamic state variable models generally consist of two parts: a 'backwards' calculation of optimal decisions for all states and time-steps, and a 'forward' simulation of individual sequences.

In **Paper IV**, we developed a dynamic state variable model to properly investigate the effect of energy reserves on optimal physiological and behavioural decisions when bats were presented with the options to go out to forage, use torpor or rest in the roost. The time horizon consisted of 30 days (~one summer month) where each day was split up into 72 timesteps, capturing a daily cycle lasting from sunrise to the following sunrise so that we could investigate individual optimal decisions across the day and night. By implementing realistic biological values for temperature-dependent metabolic rate and rewarming costs, temperature-dependent prey availabilities, light-dependent predation threats and interspecific competition costs, we performed an in-depth investigation of state-dependent decisions across time and environments. Furthermore, with such a model framework we were able to explore latitudinal effects on torpor decisions and individual energy budget managements.

4. Results and Discussion

4.1. Environmental- and state-dependent effects on torpor use

In **Paper I** we tested the interaction effects of individual body mass and size and environmental conditions on nightly torpor use in the Australian insectivorous eastern long-eared bat. Using mixed-effect models (with variance inflation factor checks to avoid issues of collinearity), we showed that bats spent more time torpid during nights with lower temperatures, and also with more rain, stronger winds and decreasing barometric pressure, as well as brighter moonlight. Our results suggest that these bats are evaluating multiple environmental cues in order to make complex adaptive decisions involving the energetic benefits of employing torpor while roosting versus active foraging given their environmental expectations of prey availabilities and relative predation risk. Furthermore, interaction effects revealed that as nightly precipitation increased, bats with shorter forearms or heavier body mass expressed more torpor. Whereas, larger changes in barometric pressure and increasing nightly wind speeds led to more torpor use in heavier bats compared to lighter conspecifics. However, body mass or size did not influence the effect of the strongest predictors, such as ambient temperature, indicating that responses driven by such environmental conditions are common for all individuals independent of their state, while other weather conditions may cause torpor responses in individual bats according to their current energy reserves.

To better understand the relationship between environmental conditions and individual energetic state, we explored optimal decisions in bats using a stochastic dynamic programming model (**Paper IV**). Our findings confirmed that temperature cycles and the strategic use of energy reserves are important factors influencing the diurnal patterns of behavioural and physiological decision-making in bats, including the strategic use of torpor. Such state-dependent behavioural strategies are in line with a behavioural ecology approach to similar studies in birds, but has not been well studied in heterothermic endotherms. However, some empirical studies reporting state-dependent effects on torpor use do exist (e.g. Wojciechowski *et al.* 2007; Matheson *et al.* 2010; Bieber *et al.* 2014; Zervanos *et al.* 2014; Sørås *et al.* 2022), demonstrating that individuals with more energy reserves tend to spend less time torpid. Such patterns were also predicted by our programming model, showing that individuals with lower energy reserves benefited more from the energy savings of torpor, while individuals with higher energy reserves profited more in some way from staying awake, and allowed us to further explore the relationships between state-dependent effects and environmental conditions across latitudes. It became apparent that state-dependent responses varied greatly with temperature conditions and revealed complex interactions during nighttime between state, temperature and photoperiod. Furthermore, the arousal costs from torpor and the benefits of being awake also largely impacted these diurnal patterns. To validate the accuracy of the model results, we compared the predictions for optimal decisions with our own empirical data on northern bats from Trondheim and Nittedal in Norway. The similarities between predictions and observations provide strong evidence that this model framework effectively captures the key factors influencing diurnal decision-making in bat physiology and behaviour. Our findings from this stochastic dynamic modelling framework therefore enhance our understanding of how bats adapt to the challenges of summer at high latitudes, and future climate change.

Thus far, the model framework developed here for small bats in summer in **Paper IV** only considers optimal decisions of non-reproductive individuals (but holds the potential of being expanded to also include reproductive bats in future studies). In **Paper V**, we investigated the interactions between environmental conditions and reproductive state on individual torpor expressions from our empirical data collected on the Norwegian brown long-eared bats. We found that lower temperatures led to more time spent torpid both during daytime and nighttime, but that pregnant and lactating females spent less time torpid during the day than non-reproductive individuals, while females in general spent less time torpid than males during the night. Increased nightly rainfall led the bats to return earlier and spend more of the night torpid, while higher wind speeds resulted in less time spent foraging at night. Overall, bouts involving deep torpor both during the day and night were frequently observed in this population of brown long-eared bats, although pregnant females generally only expressed shallow torpor and more independent of temperature conditions. Deep and/or frequent torpor use appears to be an important strategy for energy budget management during midsummer in such high-latitude populations of nocturnal bats, when foraging time is short and environmental conditions vary. However, for pregnant and lactating females that are restricted in their torpor expressions, other management strategies must perhaps be used in order to maintain a positive budget. In our data, lactating (and to some extent pregnant) females appeared to accept greater predation risk in leaving the roost considerably earlier than non-reproductive individuals, thereby likely profiting from the higher insect densities in the early night (Rydell 1992; Lima & O'Keefe 2013). Milk production is incredibly energy demanding (Kurta *et al.* 1989; Rydell 1993), and by restricting torpor use during lactation females must be better able to meet extra energy requirements through increased foraging to ensure sufficient growth of their offspring along with their own bodily maintenance. These findings suggest that bats living in challenging high-latitude environments balance their energy budgets not only through immediate responses to current conditions, but also through strategic decision-making over periods of hours if not days according to their energetic state and multiple environment variables affecting their physiology, foraging success and predation threat.

4.2. Light condition impacts on torpor and foraging decisions

In **Paper I**, we discovered indications of lunar phobia in the Australian eastern long-eared bats, where the nightly torpor use increased as a response to increased moon disk illumination. Various effects of moonlight or lunar phases on bat activity have been described in previous studies, including negative effects on bat activity and/or shifts in their foraging sites use to darker habitats (Fenton *et al.* 1977; Lang *et al.* 2006; Appel *et al.* 2017; Vásquez *et al.* 2020), positive effects on bat activity (Erickson & West 2002; Appel *et al.* 2017; Vásquez *et al.* 2020), or moon light/phases having no effects at all (Negraeff & Brigham 1995; Karlsson *et al.* 2002; Holland *et al.* 2011; Mushabati *et al.* 2022). Influences of moon illumination therefore seems highly dependent on the ecology of the species or location. A meta-analysis on moonlight avoidance by Saldaña-Vázquez and Munguía-Rosas (2013) and a review on anti-predator behaviour in bats by Lima and O'Keefe (2013) both found that lunar phobia mainly occurred in tropical habitats. In our study (**Paper I**), the positive effect of moon disk illumination on nightly torpor use was present in bats at both locations (tropical and sub-tropical). We believe these results show how moon illumination may be important for individual foraging decisions and energy budget management, potentially through increased perception of predation threat at higher illumination levels.

In **Paper IV**, we investigated the effects of photoperiod on optimal state-dependent behaviour across latitudes by using lux-measurements cycles from two locations in Norway (Trondheim and Nittedal) to describe the photoperiods. Given the main theories as to why nocturnality has evolved in bats (see section 1.3), predation threat and interspecific competition costs were included as light-dependent variables in the model and thus varied throughout the daily cycle, influencing the optimal decisions made by the bats at each timestep. With this model, we discovered that the effects of photoperiod on optimal torpor use were highly dependent upon temperature, where the bats on the coldest days spent the whole day and the following night in torpor, regardless of photoperiod (or state). However, on warmer days the photoperiod affected individual optimal torpor use, where bats of the same energetic state faced with the same temperature conditions would spend more time torpid during daytime at higher latitudes, and be more reluctant to exchange torpor use for time spent resting when not being out foraging during night time. Furthermore, light conditions appeared to be the limiting factor for bat population distributions when we explored one month survival probabilities across a latitudinal gradient (from 60.1°N to 70.9°N). Therefore, at high latitudes we conclude that the photoperiod is likely to affect individual bat behaviour and energy management and may also restrict bat species distributions from expanding further north even if climate change leads to further warming of the northern areas.

The light sensitivity in the empirical data on brown long-eared bats was investigated in **Paper V**, where we discovered that the timing of emergence from the roost at night was strongly influenced by light-levels measured at sunset, with higher lux-levels resulting in a delayed emergence, although lactating females would generally leave the roost earlier than non-reproductive individuals. Bats never left the roost during strong illumination (maximum light levels measured at emergence was 37.3 lux, while the median was 1.5), illustrating their strong sensitivity to light levels regarding the timing of foraging flights. However, although the bats generally returned to their roosts before sunrise, they tolerated drastically lighter conditions upon the return than at the emergence (maximum light level measured at the return was 1476 lux, with a median of 173.5 lux). Furthermore, light levels did not seem to influence the timing of the return, suggesting that the light sensitivity in this population of brown long-eared bats is mainly directed at the period around dusk when leaving the roost, which is likely the period in time with the highest probabilities of facing predation attempts from late-hunting diurnal raptors (Lima & O'Keefe 2013).

4.3. Similarities in torpor characteristics across climate zones

In **Paper II**, we showed that torpor metabolic rates measured across temperature ranges were strikingly similar for the Norwegian brown long-eared bats and the Australian eastern long-eared bats, although they are species inhabiting vastly different environments on separate global hemispheres. Furthermore, from recorded T_{skin} data of free-ranging individuals, we defined five daily torpor patterns that were observed throughout the datasets in both species:

1. Normothermic (no torpor bouts initiated).
2. W-shaped pattern: two torpor bouts were expressed during the day, commonly one in the morning and one in the afternoon.
3. One-bout torpor pattern: a single torpor bout expressed during the day, commonly initiated in the morning.
4. Multibout torpor pattern: the bats employed torpor at multiple (>2) occasions during the day.
5. Full-day torpor pattern: the bats spent the whole day and following night torpid.

After collecting data from the literature on bats inhabiting a range of climate zones, from tropical and desert habitats to subarctic areas, we further showed that the recorded mean minimum torpor metabolic rates and the recorded daily T_{skin} patterns revealed strong similarities despite being observed in bats living in vastly different environments. The low mass-specific minimum torpor metabolic rates recorded across species and climate zones illustrate how torpor as an energy-saving state is not limited to certain habitats. The observed similarities in torpor physiology might be driven by careful selection of roosts and microclimates, even when macroclimates across geographical locations may vary considerably.

We further discovered that the one-bout and W-shaped torpor patterns were the most common daily heterothermic patterns found across populations and climate zones. Such patterns are likely caused by daily temperature cycles (e.g. Turbill *et al.* 2003a; Turbill *et al.* 2003b), which was supported by our findings from the theoretical modelling in **Paper IV**, although these results also suggested that individual energetic state played a large role in the expressions of such daily torpor patterns.

4.4. Improving methods for determining torpor from T_{skin} data

In **Paper III** we showed that the short torpor bouts in our dataset often lacked periods of 'stable torpor', because the bats would initiate the rewarming phase before reaching a stable T_{skin} level. Furthermore, using only a strict threshold to distinguish 'torpid' from 'euthermic' values can lead to potentially large underestimations of torpor bout durations, highlighting the importance of phase-differentiation methods when applying such thresholds to identify torpor bouts in T_{skin} (or T_b) data. Although certain issues associated with the threshold method remain, such as comparisons across species (see Boyles 2019), our phase-differentiation approach improves upon current methods by allowing more reliable detection of the nature of the start and end of any torpor bout, independent of the threshold value used for initially identifying torpor. By including R codes for dividing torpor bouts into phases we also ensured that our suggested method easily can be applied to any dataset containing heterothermic T_{skin} or T_b data.

5. Conclusions and Future Perspectives

Through empirical data analyses and theoretical modelling, this thesis further extends our understanding of the interrelationships between environmental conditions, individual energy state and heterothermic expressions in bats. By exploring the effects of environmental conditions and individual state on torpor expressions and foraging decisions (**Paper I, Paper IV, Paper V**), comparing torpor characteristics across climate zones (**Paper II**), and improving existing methods for torpor determination (**Paper III**), I provide an extensive and in-depth investigation concerning strategic torpor use and energy budget management (Fig. 5), with an emphasis on high-latitude bat populations faced with challenging summer conditions.

With regards to the effects of various environmental conditions on torpor use in small insectivorous bats (**Paper I, Paper IV, Paper V**), the strong plastic responses to different conditions highlight the resilience of bats to the challenges of summer months at high latitudes. However, it also demonstrates the importance and complexity of the effects of temporary weather conditions on the management of individual energy budgets. Furthermore, our development of a stochastic dynamic model framework has allowed us to properly investigate the predicted effects of individual energy reserves across the daily cycle

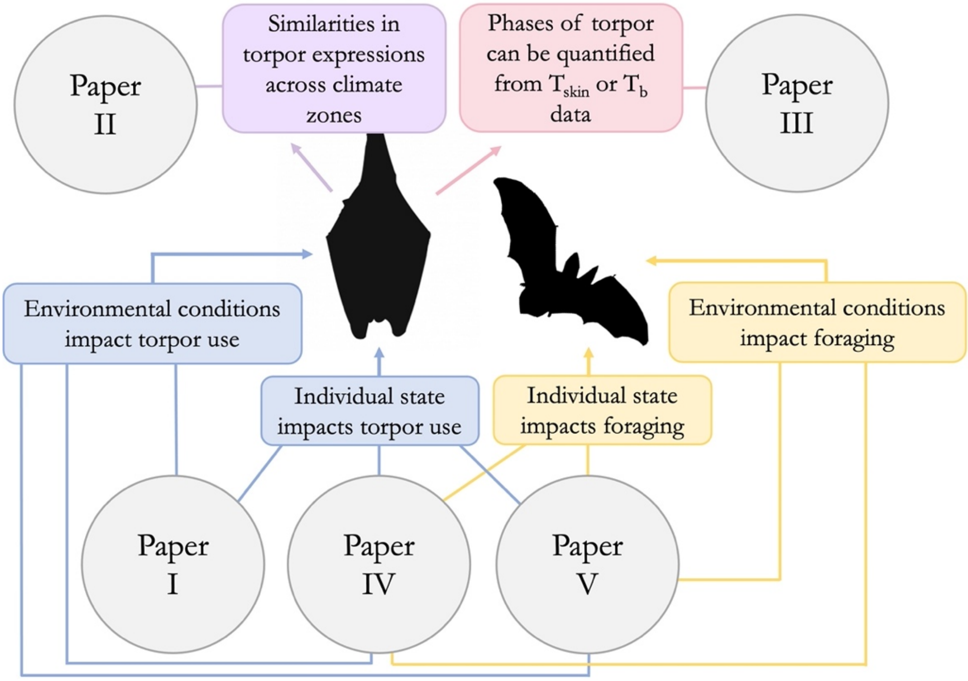

Figure 5: Simplified schematic of the main topics and results from each of the five papers in this thesis.

and its dependence upon environmental conditions (**Paper IV**). We were thus able to demonstrate how the combined effects of temperature, photoperiod and individual energetic state lead to the different contrasting diurnal patterns in torpor and foraging commonly observed in empirical studies. Importantly, these torpor patterns include specific diurnal cycles observed across the day and night in bat populations even across climate zones (**Paper II**).

5.1. Programming model potentials

The model framework of the 'small-bat-in-summer' developed as part of this thesis (**Paper IV**) offers extensive possibilities for predictive modelling of other systems and/or scenarios. R codes have been made available along with the manuscript, which allow the use of the model framework by other researchers or interested parties. Firstly, the values used to model the different populations across a latitudinal gradient in Norway can be replaced by biological values from other species or study systems in order to test alternative scenarios with the same expected state-dependent dynamics. Furthermore, extensions and alterations to the model framework would make it possible to also test for additional state-dependent trade-off scenarios in bats (or other heterotherms), such as models for individuals in different reproductive states, investigations concerning roost type choice, and/or the strategic diurnal use of various torpor depths. As such, this model framework has substantial potential for further use to better understand adaptive state-dependent decision-making across different environments, and could thus be used to model population persistence via behavioural/physiological adjustments according to various alternative climate change scenarios.

5.2. Climate change implications

In response to the ongoing global climate change, species worldwide have altered their distributional ranges, changed their migration patterns or adjusted their timing of seasonal activities, all off which has led to observations of mismatching phenologies and overall population declines (IPCC 2014; Martay *et al.* 2017). However, relative to the wide distribution and species-richness found in bats, little is known about how bat populations are affected by climate change. Attempts to investigate such effects on bat populations in Europe found either weak or inconclusive effects (Bowler *et al.* 2015; Martay *et al.* 2017). Nevertheless, bat populations worldwide are in decline, likely due to collective challenges of habitat loss, anthropogenic stressors, climate change, and diseases such as the white-nose syndrome

(Rodhouse *et al.* 2012; Frick *et al.* 2019). Heterotherms may potentially be buffered against certain costs introduced by a changing climate through alterations to their energy requirements by adjusting their use of torpor and hibernation, which are strategies that have been found to reduce extinction risk in mammal species (Geiser & Turbill 2009; Liow *et al.* 2009). However, observations of dwindling bat populations worldwide demonstrate that even the use of facultative heterothermy is not enough to shield bats completely from the current human-induced loss of biodiversity that has been termed "the sixth mass extinction" (Ceballos *et al.* 2015). The question is just how much populations of bats can mitigate these effects with their plasticity in the diurnal use of torpor and foraging excursions, and what can we do locally to help them (e.g. through provision of more favourable roost sites)?

In addition to mean increases in overall temperature conditions and short- and long-term changes to precipitation patterns, projections of future climate scenarios also point towards increased variability in weather events as a consequence, which could impact the predictability of environments (Boer 2009). The results of the empirical data analyses in **Paper I** and **Paper V** show the complex relationships between weather conditions and the energy budgets of insectivorous bats through their management of torpor expressions. This suggests that ongoing environmental changes may significantly influence individual hibernation and torpor patterns of bats across seasons and locations. With more stochastic weather conditions, it may be harder for nocturnal bats to adjust their energy budgets accordingly, particularly in light of the extreme declines in insect biomass observed across countries in recent years as a result of climate change, habitat loss and pesticide use (Goulson 2019). At the northern distribution limits of bats inhabiting high latitudes, non-reproductive bats may buffer environmental changes to an extent through their opportunistic use of daily torpor, but with strong trade-offs between torpor use and reproduction it is unclear how the combination of various stressors along with environmental change may impact the persistence of breeding colonies. Our findings from the stochastic dynamic model in **Paper IV** suggest that the photoperiod at high latitudes may be the ultimate limiting factor for high latitude bat species distributions in summertime, which means that range shifts further north in response to ongoing climate change is unlikely to be an option for bats. However, the persistence of populations immediately south of such limits could be modelled to provide management recommendations of the key factors driving extinctions under different climate scenarios.

This thesis thus provides a substantial contribution to our understanding of essential within- and among-individual strategies in bats faced with various environmental conditions, and it highlights the importance of individual state and diurnal routines in energy management and foraging under predation threat. To properly predict the consequences of climate change on bat population persistence, future studies should not overlook the importance of state-dependent effects when conducting empirical and theoretical investigations, as individual level responses may scale up to impact population level viability.

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Paper I

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BEHAVIORAL ECOLOGY – ORIGINAL RESEARCH

Nightly torpor use in response to weather conditions and individual state in an insectivorous bat

Mari Aas Fjelldal[1] · **Jonathan Wright**[1] · **Clare Stawski**[1]

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Abstract

Torpor is a well-known energy conservation strategy in many mammal and bird species. It is often employed when environmental conditions are unfavourable to maximize survival probabilities. However, torpor often carries with it the physiological costs of a low body temperature and of rewarming in addition to potential missed opportunities for foraging. Therefore, we hypothesised that decision making regarding when to use torpor should reflect the most important environmental conditions for species distributions, and thus how they may be impacted by ongoing climate change. We investigated how weather conditions affect nightly torpor patterns in the nocturnal insectivorous Australian eastern long-eared bat (*Nyctophilus bifax*). By measuring the skin temperature of 37 free-ranging individuals, we confirmed that torpor was used more frequently during the winter and at subtropical compared to tropical locations. Using mixed-effect models we show that lower ambient temperatures were the main driver of individual torpor use, probably due to lower roost temperatures and prey availability. However, increased rain, wind and humidity, and decreasing barometric pressure, as well as brighter moonlight, also led to more time spent torpid per night. We suggest that bats evaluate multiple environmental cues to make decisions regarding torpor use versus active foraging based upon their expectations of the energetic benefits, prey availability and relative predation risk. Interactions between some of these effects and body mass (whilst controlling for forearm length) indicate that individual variation in body size and/or state-dependent effects of energy reserves also partly determined the use of nightly torpor in these bats.

Keywords Energy budget · Heterothermy · Lunar phobia · *Nyctophilus bifax* · Radio telemetry

Introduction

Seasonality and daily variation in weather can inflict substantial energetic costs on endotherms that have to constantly balance their energy budget to maintain a stable body temperature (T_b). Increases of thermoregulatory and body maintenance costs during poor weather conditions result in animals needing to compensate for the energy lost, for example through increased foraging rates. However, many food sources are also seasonal or vary with weather conditions, which for many species can lead to a mismatch between energy requirements and resource availability. In a range of endotherm species we, therefore, find strategies such as daily torpor and hibernation (temporal heterothermy) that are characterized by reductions in metabolic processes and a decrease in T_b (Ruf and Geiser 2015). The energy requirements of torpid animals are thus greatly reduced and allow them to save energy when foraging opportunities are scarce or energetically costly to pursue. Importantly, the chance of survival may be enhanced by torpor use, for example by decreasing foraging requirements and exposure to predators (Geiser and Brigham 2012). However, arousal from these states has been identified as energetically costly or physiologically challenging in many species (Currie et al. 2015; Landes et al. 2020). Therefore, for the use of daily torpor to be effective in managing energy requirements, animals need to balance the costs and benefits of torpor use against the benefits of foraging and the risks of predation and starvation (Jastroch et al. 2016).

Hibernation and daily torpor are widespread strategies in bats (Chiroptera). Due to their extreme energetic demands for maintaining flight, echolocation and thermoregulation (Lyman 1970; Winter and Von Helversen 1998; Currie et al.

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✉ Mari Aas Fjelldal
mari.a.fjelldal@ntnu.no

[1] Department of Biology, Norwegian University of Science and Technology (NTNU), 7491 Trondheim, Norway

2020), many bats are highly dependent upon temporal heterothermy to save energy during inclement conditions. Many bats are insectivorous, and thus depend upon food that varies seasonally with ambient temperature and weather (Stawski 2012a). The typical decreases in insect activity during winter have in previous studies been linked to a general reduction in the activity levels of bats during winter compared to summer (Richards 1989; Stawski and Geiser 2010b). As a result, seasonality is often used as a proxy for thermal conditions and for food availability and is, therefore, seen as a driver of torpor patterns (Wojciechowski et al. 2007; Geiser 2020). Food availability being a driver in itself is particularly evident when considering the contrary seasonal torpor patterns of the nectivorous subtropical blossom bat (*Syconycteris australis*), which uses more torpor during summer than winter as the flower nectar they feed on is more abundant during winter (Coburn and Geiser 1998).

For insectivorous bat species, multiple environmental conditions besides T_a have been found to affect nightly activity levels and foraging intensity. This includes effects of variation in precipitation, wind speed, humidity, barometric pressure and moonlight (Fenton et al. 1977; Paige 1995; Erickson and West 2002; Lang et al. 2006; Turbill 2008; Wolcott and Vulinec 2012; Appel et al. 2017), which have been linked to physiological or thermoregulatory costs, decreases in food abundance or increased predation risk, respectively. However, environmental conditions are not the only drivers of temporal patterns in activity and torpor. Behavioural decisions linked to trade-offs in energy allocation are strongly connected to the current state of an individual (McNamara and Houston 1996). State-dependent foraging behaviour and torpor use in bats have previously been linked to individual reproductive state (Hamilton and Barclay 1994; Mackie and Racey 2007), severity of infections (Reeder et al. 2012), and individual body condition (Park et al. 2000; Stawski and Geiser 2010a). Thus, in order to understand torpor decisions made at the individual level, both environmental conditions and individual state need to be considered.

With this study we aimed to explore what underlies the balance between nocturnal torpor use and foraging in insectivorous bats, using a large dataset collected on the eastern long-eared bat (*Nyctophilus bifax*). This is an insectivorous bat species endemic to the subtropical and tropical regions of Australia and has previously been found to employ torpor across seasons and climate zones (Stawski and Geiser 2010b; Stawski 2012b), indicating possible common individual torpor responses to changes in environmental conditions. Most studies investigating environmental effects on nightly bat activity tend to measure activity based upon capture rates, echolocation frequencies or emergence numbers from roosts. In this study, we instead explore the effect of nightly conditions on individual torpor use, which as a direct physiological response differs from indirect measures of activity levels (Wojciechowski et al. 2007; Salinas et al. 2014). Torpor use should thus tell us more about how these bats evaluate prospective foraging conditions and the relative costs and benefits to their energy budget and life history in order to employ torpor at specific times. We tested the hypothesis that torpor should be consistently used as a sensible response to inclement conditions that are likely to affect prey abundance and/or the bat's energy expenditure in flight, as this would limit potential benefits of foraging. Additionally, we hypothesized that individual state and perceived predation risk (using moon illumination as a proxy here) would also impact nightly torpor use, again due to shifts in the balance between costs and benefits of active foraging versus rest using torpor.

Materials and methods

Data collection

Eastern long-eared bats were captured across seasons at one subtropical and one tropical field site in Australia between 2007 and 2009. At the southern subtropical location at Iluka Nature Reserve (New South Wales, 29°24′ S, 153°22′ E) bats were captured during the austral winter (July–August 2007, $N_{ind} = 8$), summer (February–March 2008, $N_{ind} = 12$) and spring (October–November 2008, $N_{ind} = 6$). At the northern tropical location in Djiru National Park (Queensland, 17°50′ S, 146°03′ E) bats were captured during two consecutive winters (June 2008, $N_{ind} = 5$; July–August 2009, $N_{ind} = 6$). The climate characteristics varied between the two sites, with the subtropical location (weather station number 058012) generally experiencing colder T_a (mean minimum and mean maximum T_a being, respectively, 9.7 and 19.1 °C in July, and 20.4 and 26.8 °C in February) than the tropical location (weather station number 032037; mean minimum and mean maximum T_a being respectively 15.2 and 23.9 °C in July, and 22.8 and 30.8 °C in February) when looking at climate statistics for the last 75–140 years (Australian Bureau of Meteorology). The subtropical location also received less than half of the mean annual rainfall (1462 mm) compared with the tropical location (3283 mm).

Permits for this study were approved by the University of New England Animal Ethics Committee (AEC08/046 and AEC09/058), New South Wales National Parks and Wildlife Service (no. S12448), and Queensland Parks and Wildlife Service (WITK04955708). Bats were captured using mist-nets placed within openings in the rainforest or across pathways. After capture, we trimmed a small patch of fur from the mid-dorsal region and attached a temperature-sensitive transmitter (~ 0.5 g, LB-2NT, Holohil Systems Inc., Carp, Ontario, Canada) with a skin adhesive (SkinBond, Smith and Nephew United, Mount Waverley, NSW, Australia). The bats were released at the capture site and tracked to their roost where we placed an antenna and a remote logger (Körtner and Geiser 1998), recording pulse intervals from the transmitters every 10 min. We calibrated transmitters between 5 and 40 °C in a water bath prior to attaching them to the bats, and the logged pulse intervals could afterwards be converted to skin temperatures (T_{skin}).

Data variables

From the T_{skin} data we estimated nightly torpor use. Previous studies have suggested that $T_{\mathrm{b}} < 30.0$–31.0 °C should be defined as torpor events (Barclay et al. 2001). With $T_{\mathrm{b}} - T_{\mathrm{skin}}$ typically being < 2.0 °C for small mammals, we defined torpor bouts as a period of more than 30 min with T_{skin} below 28.0 °C. We acknowledge the issues with using a single cut-off value to define torpor bouts (see Boyles et al. 2011). However, other methods also introduce uncertainty, and no consensus has been reached for deciding on the best method to determine torpor from T_{skin} measurements alone. Importantly, the bats in our study employed torpor bouts that decreased T_{skin} well below 28 °C in most cases, and although we cannot guarantee that there were no overlooked shallower torpor bouts, we believe this to be less likely during night-time than day-time due to generally lower T_{a} values (the nightly T_{a} ranges in our dataset were 4.0–22.6 °C in winter, 10.0–22.5 °C in spring, and 17.0–25.5 °C in summer). See Fig. 1 for visual examples of torpor bouts expressed at the tropical (Fig. 1a) and subtropical location (Fig. 1b). Nightly torpor use was estimated as the total duration in minutes spent torpid between sunset and sunrise. We obtained sunset and sunrise data from the geodetic calculator on the Geoscience Australia webpage. 270 bat nights were recorded across the 37 individuals; 151 nights for females ($N = 20$) and 119 nights for males ($N = 17$). Number of nights recorded per individual ranged from a single night (3 females and 2 males) up to 19 nights for females and 26 nights for males, with the median being 7 for the females and 4 for the males.

The Australian Bureau of Meteorology provided us with weather variables, including hourly precipitation, relative humidity, windspeed, and barometric pressure (BP). Additionally, we recorded environmental temperature (°C) at 10-min intervals using temperature-sensitive data loggers (0.5 °C, DS 1921G Thermochron iButtons, Maxim Integrated Products, Inc., Sunnyvale, CA, USA) placed outside of bat roosts at the data-collection sites. One last predictor, the percentage of moon disc illuminated, we obtained from the lunar calendar through the Calendar Australia webpage. Unfortunately, this variable does not account for potential additional variability in illumination caused by cloud cover, due to lack of data on this combination of factors. The different environmental variables were all considered relevant to include in our analyses as they have been found to impact foraging behaviour or physiological costs in small bats (see "Discussion" for

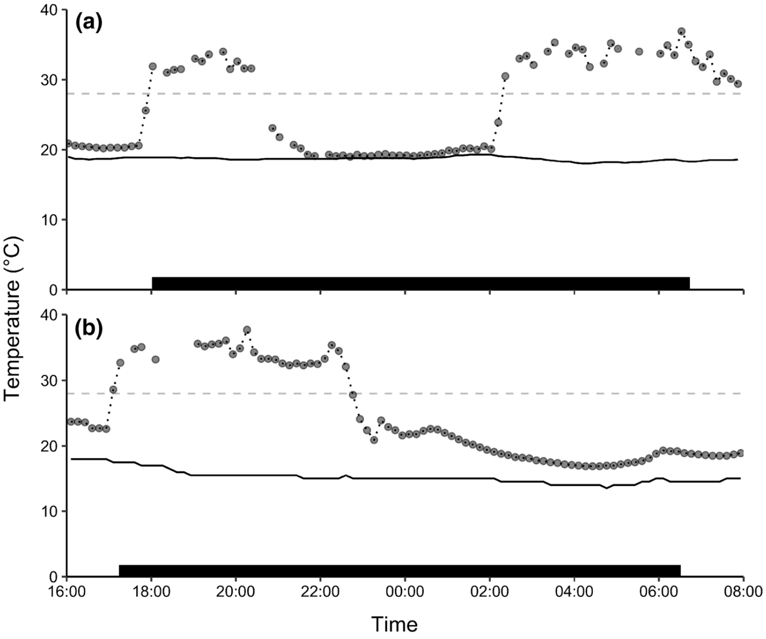

Fig. 1 Skin temperature (T_{skin}) patterns of two female eastern long-eared bats (dotted lines) over one measured winter night to illustrate torpor bouts expressed **a** at the tropical location and **b** at the subtropical location. Solid lines show the measured ambient temperature (T_{a}) outside the roosts, and the horizontal dashed lines indicate the torpor cut-off value used here of 28 °C. The black bars at the bottom represent the night-time period between sunset and sunrise

literature citations). Each variable except moon illumination was converted into six versions: mean nightly condition, the standard deviation of the mean nightly condition, the maximum and minimum hourly value during the night, the range between the minimum and maximum value, and accumulated values throughout the night. Additionally, from the mean BP data variable, we created a ΔBP variable which captured the change in mean barometric pressure from the previous night.

Statistical analyses

We performed analyses in the software R (version 3.5.2). All numerical variables were scaled and centred through the *scale* function. For data reduction purposes and to avoid model over-fitting, we performed principal component analyses (PCA) followed by a varimax rotation with the *principal* function from the "psych" package (Revelle 2017). However, none of the PCA models revealed any clear structure in the covariances that could be used to extract composite weather measures. We, therefore, continued with the analyses using only the nightly mean and range weather variables, keeping in mind the levels of covariance already identified (see Supplementary Materials 1 for covariance matrices).

We constructed linear mixed-effect models using the *lmer* function from the "lmerTest" package (Kuznetsova et al. 2017), with individual ID and date ID as random effects. Proportions of variance explained by the random effects were calculated using the *get_variance* functions from the "insight" package (Lüdecke et al. 2019). The effects of season and location on torpor use were tested separately and could not be included together in further models due to imbalance in the dataset (only winters were measured at the tropical location). The effect of night length was tested for but was excluded from further models as the limited variation in this variable had no apparent effect on nightly torpor use. We first constructed preliminary models including the various environmental variables by separately testing the mean and the range version of each variable to examine which was a better fit for further model selection. During this stage we also tested for non-linear quadratic effects, but there were none. We thus identified that the mean and linear versions of each of the numerical environmental variables that best explained variation in torpor use and proceeded to construct a global mixed-effect model. The nightly mean for the numerical variables ranged from 6.0 to 23.4 °C for T_a (scaled range − 2.06 to 1.85); 0.0 to 1.5 mm for precipitation (− 0.32 to 5.18); 3.9 to 32.2 m/s for windspeed (− 1.75 to 3.25); 998 to 1022 hPa for BP (− 2.92 to 2.04); − 10.0 to 6.7 hPa for ΔBP (− 3.15 to 2.18); 38.5 to 96.1% for humidity (− 2.67 to 1.38); 0 to 100% for moon size (− 2.17 to 1.36).

The original global model

The original global model on the scaled raw data variables included all two-way interactions between the different fixed effects: T_a, sex, precipitation, humidity, windspeed, BP, ΔBP, and moon size. In order to investigate collinearity-issues in the models, we noted the variance inflation factor (vif) using the *vif* function from the "car" package (Fox and Weisberg 2018). Commonly, vif-values should be < 5 to avoid the need for correcting measures and < 10 to avoid removal of one of the correlated explanatory variables, although these limits have been disputed (O'Brien 2007). As the most complex models had strong collinearity issues, we performed model reduction based not only on *P* values and AIC-ranking (Forstmeier and Schielzeth 2011), but also on vif-values in the early stages of the model selection. The maximum vif-value for each of the ten highest ranked models are listed in the model selection tables (Supplementary Materials 2). A model was considered a better fit when the ΔAIC was reduced with > 2 (Burnham and Anderson 2002). In cases where two models had ΔAIC < 2, the model with the least degrees of freedom was considered the better fit, based on the concept of parsimony.

Within- versus among-subject effect models

As the individuals in this study were measured across two study sites and during different seasons, different individuals will have faced different average environmental conditions during data collection. However, we were primarily interested in any common reversibly plastic responses to environmental cues (i.e. within-subjects effects), as opposed to these among-subjects effects driven mainly by the mean differences in environmental conditions experienced by the different individuals. We, therefore, applied the methods described in van de Pol and Wright (2009) to our data in order to decompose within- versus among-subject effects in mixed models. Unfortunately, convergence issues (largely due to the among-subjects variation) prevented us from applying all aspects of the method to the original global best model, due to its complexity and various interaction terms (see "Results"). We, therefore, performed separate model selection (as above) for just the within-subjects effects in order to see if it included the same predictors as the original combined-effect best model. Similar model selection for just the among-subjects effects again resulted in serious model convergence issues that could not be resolved, probably due to the unbalanced data set in this case. We therefore performed the decomposition of within- versus among-subjects effects, as recommended by van de Pol and Wright (2009), on 7 separate and simpler models, each including temperature (as expected, T_a was the main predictor) and one other environmental variable (see Supplementary Materials 3).

State-dependence

Forearm length and body mass were each added as interaction effects with every predictor in the best original model and in the best within-subjects effect model. We did not create or test specific body condition index metrics, as this method has been the subject of widespread concern regarding its statistical and biological validity (García-Berthou 2001; Wilder et al. 2016). Instead, the effect of body condition was assessed via the effect of body mass in the models that also controlled for the effect of skeletal body size in the form of forearm length. Forearm length and body mass were not significantly correlated (see Supplementary Materials 5) and could safely be included together in all models. However, correlation issues emerged when including forearm and body mass together with sex in the models, as females in this dataset have significantly larger forearms ($P < 0.01$) and are significantly heavier ($P < 0.001$) than males. Thus, in order to test for the state-dependent effects of body size or body condition (i.e. body mass controlling for body size) we excluded sex from the models before proceeding to the model selection process. The body mass of the three pregnant females was not included in these analyses, as in these cases it represented more than energetic state in the form of fat reserves.

We also tested for potential effects of weather conditions from the previous night ($t - 1$) as this could affect the individuals' current state at time t. We performed additional model selection using the best within-subjects variance model, where we added the environmental conditions at time $t - 1$ (T_a, precipitation, humidity, windspeed, BP, ΔBP, and moon size) using the same model structure as with the environmental variables at time t, with all effects being simple additive ones, except for the precipitation–sex interaction. However, the presence of temporal autocorrelations between successive values of the different weather variables could result in apparent temporal autocorrelations in individual behaviour, leading to non-random residuals around individual temporal trendlines (Mitchell et al. 2020). Indeed, moon size, barometric pressure and humidity showed heavy temporal auto-correlations between the t and the $t - 1$ variables (see Supplementary Materials 5), restricting us to only applying one of each variable at time t. Additionally, we included torpor use at time $t - 1$ to investigate if there was any residual variation in individual torpor linked to the previous night use that was not explained by the environmental variables from a current or previous night.

Results

General results

Nightly torpor use in these eastern long-eared bats varied greatly and ranged from no torpor use to spending the full night torpid (0 to 818 min). The mean nightly individual torpor use was 294.9 ± 259.8 min ($N_{\text{nights}} = 270$, $N_{\text{ind}} = 37$).

Seasonal differences could only be tested with data from the subtropical location ($N_{\text{nights}} = 197$, $N_{\text{ind}} = 26$) and revealed a high seasonal variation in nightly torpor use (Fig. 2a). Mean individual nightly torpor use during spring and summer was not significantly different (spring 82.2 min, SE ± 58.1; summer 166.9 min ± 71.1; $P = 0.25$) but was significantly lower than the torpor use seen during the winter (692.5 min ± 76.8; $P < 0.001$). The difference in torpor use between the two locations could only be analysed using data from the winter ($N_{\text{nights}} = 210$, $N_{\text{ind}} = 19$) and showed a significantly ($P < 0.001$) higher individual mean nightly torpor use at the subtropical (692.5 min ± 42.9) compared to the tropical location (261.6 min ± 56.3; Fig. 2b).

The original model

The overall model using the original variables that best explained the variation in nightly torpor use included all the explanatory variables plus several interactions (see Table 1, and Table S2.2 in Supplementary Materials 2 for the 10 highest ranked models). The random effect here of individual ID explained 5% of the total variation in torpor use, and day ID explained 3%, suggesting that the fixed effects included in this model explain the majority of the variation. Environmental variables that had a negative effect on nightly torpor duration included temperature and barometric pressure. Positive effects included precipitation, wind speed, ΔBP, humidity, and moon size. Additionally, females spent approximately an hour longer in torpor during the night than males. The interactions included a sex–precipitation effect where the positive precipitation effect on males was significantly stronger than on females. Additional interactions from the best model included a T_a:ΔBP effect, a humidity:wind speed effect, a humidity:BP effect, and interactions between moon size and precipitation, BP, ΔBP, and humidity. See Table 1 for exact values and Fig. 3 for graphical presentations of these main results from the model. The interaction effects that included two weather condition predictors are presented graphically in Supplementary Materials 3 (Fig. S3.1). The scaling of the numerical values here allowed us to directly compare the estimated effects of each predictor on the nightly torpor

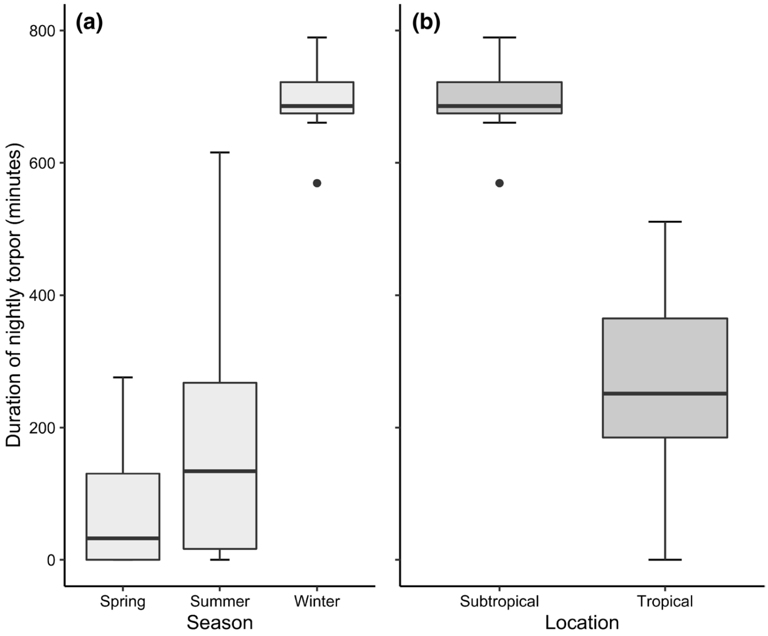

Fig. 2 Individual nightly torpor use measured in eastern long-eared bats across seasons and locations. **a** Analyses of seasonal differences from the subtropical location revealed that the mean duration of torpor during the night was non-significantly different between spring and summer, but with significantly higher torpor use during winter. **b** The two locations measured during the winter season differed significantly in nightly mean torpor use with more nightly torpor expressed in the subtropical location compared to the tropical. Thick bars indicate median values, shaded boxes interquartile ranges, and whiskers the largest or smallest values within 1.5 times the interquartile ranges, with dots showing outlying values

duration in eastern long-eared bats. Nightly mean temperature (T_a) was by far the strongest predictor, estimating an effect size more than four times larger than the second largest effect size.

Within- and among-subjects effect models

The model selection of the within-subjects effects using individually mean-centred variables led to a simpler best model than the original model (above). All additive effects were still present in the final model, but of the interactions only the sex–precipitation interaction remained (Fig. 4). The sex effect was not significant by itself, but it had a significant interaction effect with precipitation, where males showed a stronger response to precipitation than females. Females were not significantly affected by precipitation. Similarly to the original model, the strongest predictor by far was the nightly T_a, almost five times stronger than the second strongest predictor, which was humidity. The precipitation, barometric pressure and wind speed also showed strong effects on nightly torpor use (the precipitation effect was only significant on males), followed by moon size. Except for the non-significant effect of precipitation on females, ΔBP had the lowest effect size of the included parameters. See Table 2 for values and details.

In order to compare within- versus among-individual effects, we had to produce simpler models where we tested each variable separately (see "Methods"), and the results from each of these can be found in Supplementary Materials 4. Figure 5 illustrates the similarities between the overall additive effects from the original best model (Table 1) and the corresponding within- and among-subjects effects retrieved from these simple models. T_a remains the strongest predictor of nightly torpor use in eastern long-eared bats, indicating that all individuals responded in a similar manner to temperature changes, despite having been measured at different seasons and locations. Precipitation, another strong predictor, showed a significantly stronger among-subjects effect than within-subjects effect, although both effects were positive and significant in themselves. Different individuals, therefore, seem to respond by increasing nightly torpor use with increasing levels of precipitation, but part of the effect from the original model is caused by among-subject effects. However, as sex is not accounted for in the simple model it could explain part of why the among-subjects effect is greater than the within-subjects effect, as females were not significantly affected but males were. Another predictor revealing a difference in the effects was the ΔBP effect. The ΔBP effect from the original model was positive, which was also the case for the best within-subjects model, but the within- and between-subject ΔBP effects derived from the simpler model were slightly negative. This indicates that there are potential correlational issues with this variable that causes it to change its effect when it is modelled together with just T_a versus with additional predictors included. The remaining predictors showed similar original, within- and

Table 1 Estimates, standard error and *P* values of each explanatory variable included in the best model using the original variables, where the numerical predictors are scaled for direct comparison of their effect sizes on nightly torpor duration in eastern long-eared bats

Variable	Estimate	Std. error	*P* value
Random effects			
Day ID	0.03	0.0006	
Individual ID	0.05	0.0007	
Residual	0.08	0.001	
Fixed effects			
Intercept ♀	440.8	19.4	< 0.001
Intercept ♂	374.9	26.3	< 0.05
T_a	– 288.3	15.0	< 0.001
Humidity	64.4	14.6	< 0.001
BP	– 47.8	10.6	< 0.001
ΔBP	29.4	9.6	< 0.01
Wind speed	28.3	13.0	< 0.05
Moon size	28.1	9.4	< 0.01
Precipitation ♀	29.1	13.0	< 0.05
Precipitation ♂	65.1	11.6	< 0.01
Moon size: humidity	44.1	10.1	< 0.001
Moon size: precipitation	– 39.9	16.7	< 0.05
Moon size: ΔBP	30.5	10.7	< 0.01
Humidity: BP	27.0	12.0	< 0.05
Humidity: wind speed	– 25.7	12.8	< 0.05
Moon size: BP	– 23.6	11.1	< 0.05
T_a: ΔBP	– 22.1	7.9	< 0.01

The *P* values of the intercept and precipitation effect for males (♂) signifies whether the effects are different from the effect for females (♀). Day and individual ID were fitted as random effects and are given as the proportion of total variation explained

between-subjects effects, with only small differences (Fig. 5), revealing no apparent issues regarding correlation or over-fitting.

State dependence

State dependence in the original model

The best original model including state variables contained the same interaction terms as the original model without state variables (Table 1), except for the moon:BP effect and the moon: ΔBP effect which were not present in the state-variable model. Additionally, the state-variable model included interactions between forearm length and precipitation and between body mass and wind speed, although forearm length and body mass did not show any significant effects on their own. This indicates that individuals with larger forearms (controlling for body mass) were more affected by precipitation than smaller individuals regarding the use of torpor at night, while individuals with a larger body mass (controlling for forearm length) were more affected by increasing nightly wind speeds. Effect sizes from the state-variable model are listed in Table 3, and graphical visualisations are shown in Figure S4.1.

State dependence in the within-subjects model

The best within-subjects model (Table 4), like the best original state-variable model (Table 3), showed no direct effects of body mass and forearm length, but included several interaction effects between the state variables and environmental effects as follows: individuals with shorter forearms or heavier body mass compared to conspecifics used more torpor during the night when precipitation levels increased, while individuals with a heavier body mass used more torpor with increasing wind speeds and ΔBP levels than light individuals (see Table 4 and Fig. S5.2). The best within-subjects model did not include any of the interaction terms between two environmental variables that were found in the best original state-variables model, but included two interaction terms that were not present in the original model. These were the body mass:precipitation effect and the body mass: ΔBP effect, revealing effects that may have been camouflaged in the original model by sex and overall environmental differences across seasons and locations. The two interaction terms present in both models (body mass:wind and forearm length:precipitation) showed similar effect sizes across the two models, although the forearm length:precipitation effect was slightly stronger in the within-subjects model, indicating that these effects are not caused by any among-subjects effects.

To further investigate possible state dependency, we also tested the effect of environmental conditions at time $t-1$ to see if conditions on a previous night (and thus acquired individual differences in state) affected torpor use on the current night while accounting for current conditions. These analyses were complicated by a certain amount of temporal autocorrelations within some of the explanatory variables (Table S5.1 and Fig. S5.3). However, no $t-1$ effects of these environmental variables could be identified, None of the models showed signs of state-dependent responses to the strongest predictor, nightly T_a, which suggests that all individuals are equally affected by changes in temperature, regardless of their state. Nevertheless, scaled torpor use at time $t-1$ did show a significant effect when included in the best within-subjects effect model (18.9 ± 6.8, $P < 0.01$, ΔAIC = – 5.8), where increasing levels of torpor on a previous night positively explained some of the residual variation in torpor use at time t (Fig. S5.4).

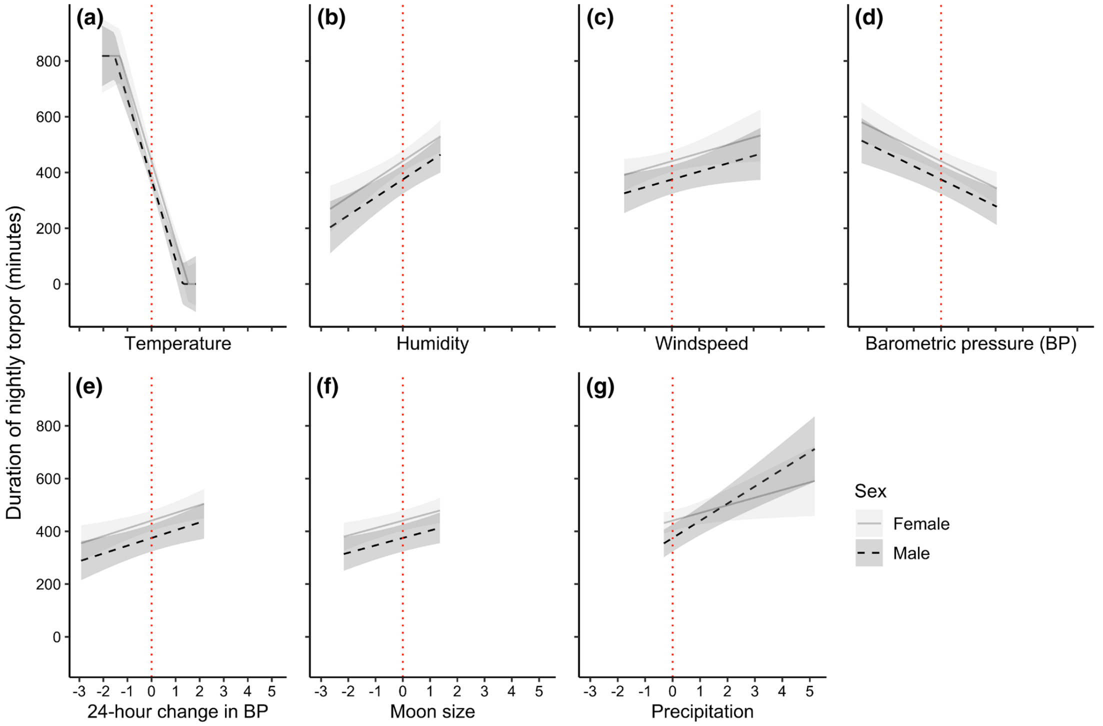

Fig. 3 The main explanatory variable effects from the best model using the original variables (see Table 1) of **a** temperature, **b** humidity, **c** windspeed, **d** barometric pressure, **e** change in barometric pressure, **f** moon size, and **g** precipitation on the nightly torpor use in eastern long-eared bats, with the red dotted line indicating zero-centred values for each of these scaled predictors. Effects are shown for both males (black dashed best-fit lines and dark 95% CI shading) and females (grey solid best fit lines and light grey 95% CI shading). Only the precipitation-effect includes an interaction with sex, where the effect is stronger in males than in females

Discussion

In this study we statistically disentangled the effects of multiple environmental factors on nightly torpor use on individual free-living bats across seasons and locations. The results reveal that Australian eastern long-eared bats use a variety of cues concerning the duration of their torpor use at night. As expected, mean nightly ambient temperature was by far the strongest predictor, more than four times larger than the second strongest predictor. The strong temperature effect across all individuals regardless of season, sex or state neatly explains the effects here of season and location. It also supports earlier findings of temperature being one of the main drivers of torpor behaviour in small endotherms, either due to the direct impact on thermoregulatory costs and/or by the indirect effect T_a has on insect prey availability (Twente and Twente 1965; Richards 1989; Ruf and Geiser 2015). However, the bats also responded by altering their nightly torpor use to environmental conditions like rain, wind, humidity, barometric pressure, and moon disk illumination, including some complex interactions between these effects. These results became clearer and more straightforward to understand when we considered only within-individual variation in these effects. We also found indications of state-dependent effects on torpor use, where body size moderated these individual responses to weather conditions, such as precipitation, windspeed, and change in barometric pressure. Contrary to what is currently known about torpor use during the resting phase in bats, we show here results indicating that torpor might be abandoned in face of too low energy reserves, as well as during inclement conditions like heavy rain or strong winds. Body size or state did not, however, affect the strongest responses involving ambient temperature, which remained the single main and unconfounded predictor of torpor use in these populations. Such a strong predictor, therefore, seems to affect individuals independent of their state, while other weather conditions may be evaluated by individuals based on their current state, such as fat reserves.

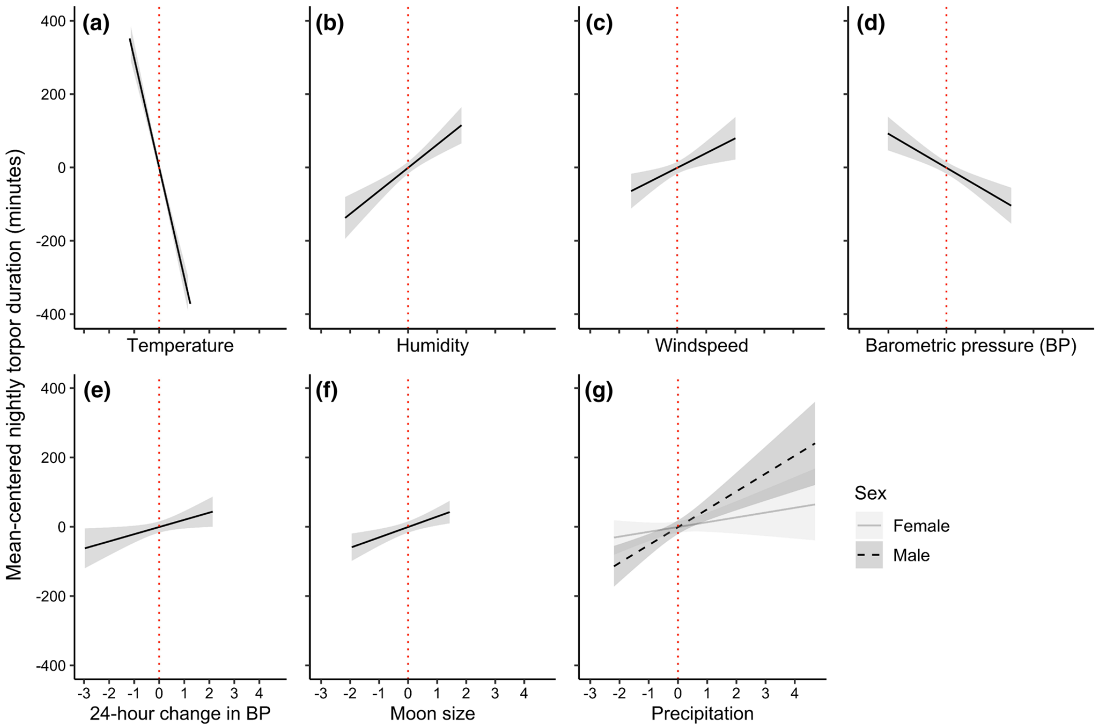

Fig. 4 Within-subjects effects from the best model using individually mean-centred variables (see Table 2) of **a** temperature, **b** humidity, **c** windspeed, **d** barometric pressure, **e** change in barometric pressure, **f** moon size, and **g** precipitation on the nightly torpor use in eastern long-eared bats, with the red dotted line indicating zero-centred values for each of these scaled predictors. The precipitation-effect includes an interaction with sex, where the effect is non-significant in females (grey solid best fit lines and light grey 95% CI shading) but significant in males (black dashed best-fit lines and dark 95% CI shading)

Table 2 Estimates, standard error and *P* values of each variable included in the best within-subjects model based on individually mean-centred variables

Variable	Estimate	Std. error	*P* value
Random effects			
Day ID	0.10	0.002	
Residual	0.31	0.004	
Fixed effects			
Intercept ♀	− 0.7	8.3	0.93
Intercept ♂	− 1.3	10.1	0.96
T_a	− 298.9	19.9	< 0.001
Humidity	63.0	12.9	< 0.001
BP	− 46.3	10.7	< 0.001
Wind speed	40.1	14.2	< 0.01
Moon size	30.0	9.7	< 0.01
ΔBP	20.7	9.5	< 0.05
Precipitation ♀	13.9	11.1	0.21
Precipitation ♂	51.5	12.9	< 0.01

As torpor use is mean-centred for each individual, the intercept is approximately 0 and Individual ID was excluded as a random effect

In contrast to the clear unconfounded effects of ambient temperature, the effects of precipitation were either sex, size or state dependent. Females were not significantly affected by variation in nightly rain conditions, while males increased their nightly torpor use with increasing precipitation levels. Replacing the sex–precipitation interaction term with body mass:precipitation and forearm length:precipitation in the best within-subject models improved the AIC value by 8.4. These interactions were also present at the within-subjects level, suggesting that these effects are in fact state- or size-dependent and not just driven by sex-specific differences. Similar individual state-dependent torpor responses have previously been found in mouse lemurs (Kobbe et al. 2011). Our findings indicate that smaller (male) bats with greater fat reserves might be able to respond to rainy conditions by saving stored energy and entering torpor, while larger (female) bats with lower levels of fat reserves cannot afford this and stay aroused to possibly take advantage of the opportunity to forage in between rain showers. It has been suggested that precipitation affects the activity levels in bats

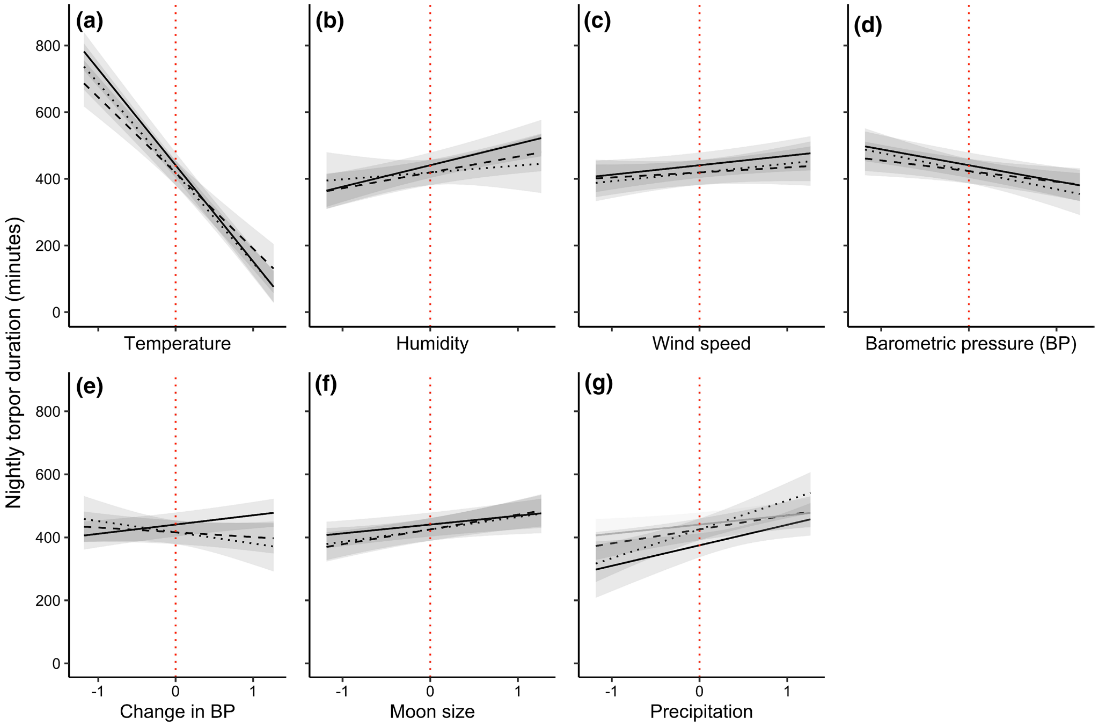

Fig. 5 Comparing the original model effects (Table 1, solid lines and light grey CIs) with within-subjects effects (dashed lines and dark grey CIs) and among-subjects effects (dotted lines and medium shaded CIs) from simple models of **a** temperature, **b** humidity, **c** windspeed, **d** barometric pressure, **e** change in barometric pressure, **f** moon size, and **g** precipitation on the nightly torpor use in eastern long-eared bats. The effect of precipitation includes an interaction with sex, where the gray solid line represents females and the black solid line represents males. Red dotted lines indicate zero-centred values for each of the scaled predictors

due to it interfering with the bats' ability to echolocate and thus detect their prey (Griffin 1971) and by increasing their thermoregulatory demands as wet fur reduces its insulation value (Tuttle and Stevenson 1982). However, other studies have found that some rain conditions (mainly light or moderate precipitation) did not reduce activity levels in insectivorous bats (Kunz 1973; Hałat et al. 2018), perhaps because aerial insect abundance does not always decline during all types of rainfall in all habitat types. Even though precipitation has been investigated as a predictor of foraging activity in insectivorous bats, there is a lack of information about the effect of precipitation on bats' use of nightly torpor. It is possible that the lack of response in torpor use to increasingly rainy conditions in females or bats with lower fat reserves does not necessarily mean that they spent more time foraging, because we did not analyse the time individuals spent away from the roost. However, as rainy conditions often vary in intensity throughout a day or night it is possible that these bats stayed aroused in order to benefit from potential rapid shifts in the weather. This was observed in a study by Fenton et al. (1977) where bat activity was supressed on rainy nights but only until the precipitation had tapered off, at which point bat activity resumed.

Wind speed may also rapidly shift in intensity throughout the night, which the mean wind condition variable will not have accounted for in our analyses. Wind speed has previously been found to negatively impact activity level in insectivorous bats (Avery 1985; Wolcott and Vulinec 2012) as well as increasing torpor expression in fishing bats (Salinas et al. 2014). The suggested mechanisms behind the effect of wind is that it functions as a source of increasing flight cost (Norberg 1990) and may also affect prey abundance by decreasing the number of flying insects (McGeachie 1989; Møller 2013). Increasing mean nightly wind speed lengthened the duration of nightly torpor in our eastern long-eared bats, but this effect was again dependent on individual body mass, both among and within individuals. As with precipitation, bats with lower body mass (while controlling for forearm length) did not respond to changes in mean nightly wind speed, while relatively heavier individuals with presumably

Table 3 Estimates, standard error and *P* values of each variable included in the best model using the original explanatory variables, and including state-variables forearm length and body mass in place of sex

Variable	Estimate	Standard error	*P* value
Random effects			
Day ID	0.04	0.0007	
Individual ID	0.05	0.0007	
Residual	0.07	0.0009	
Fixed effects			
Intercept	403.3	18.4	<0.001
T_a	– 272.2	17.4	<0.001
Humidity	44.8	16.7	<0.01
Moon size	29.8	13.3	<0.05
Precipitation	59.2	14.0	<0.001
Wind speed	27.1	14.6	0.07
BP	– 37.4	12.7	<0.01
ΔBP	24.2	12.4	0.06
Forearm length (FA)	22.9	15.4	0.15
Body mass (BM)	9.1	17.1	0.60
BM: wind	40.5	11.4	<0.001
FA: precipitation	– 20.4	5.2	<0.001
Humid: BP	40.5	16.1	<0.05
Humid: wind	– 36.7	15.2	<0.05
Humid: moon	32.6	13.4	<0.05
Moon: precipitation	– 59.4	18.6	<0.01
T_a: ΔBP	– 24.8	10.2	<0.01

Table 4 Estimates, standard error and *P* values of each variable included in the best within-subject model using individual mean-centred variables, including state-variables forearm length and body mass in place of sex

Variable	Estimate	Standard error	*P* value
Random effects			
Day ID	0.12	0.002	
Residual	0.23	0.003	
Fixed effects			
Intercept	– 4.8	7.9	0.60
T_a	– 312.9	21.3	<0.001
Humidity	65.9	14.2	<0.001
Moon size	54.6	11.7	<0.001
Precipitation	39.5	11.1	<0.001
Wind speed	38.5	15.8	<0.05
BP	– 31.4	11.8	<0.01
ΔBP	19.0	10.8	0.08
Forearm length (FA)	3.0	5.8	0.61
Body mass (BM)	0.6	8.9	0.95
BM: wind	37.1	17.7	<0.05
BM: precipitation	31.3	14.2	<0.05
FA: precipitation	– 28.9	5.9	<0.001
BM: ΔBP	23.1	9.4	<0.05

greater fat reserves responded by using more torpor on more windy nights. It, therefore, appears that individuals with more fat reserves may have saved energy using extended bouts of torpor on nights with rain and strong winds, while individuals with less fat reserves are forced to forage or just stayed aroused, possibly to be ready to forage following shifts in the weather or even to forage regardless of conditions.

Barometric pressure is a variable that does not change as rapidly as precipitation or wind conditions, but indicates more general shifts in the weather. Somewhat surprisingly, higher nightly barometric pressures led to less torpor in our bats, but with few sex- or mass-dependent interactions with this effect. Conversely, a falling barometric pressure turned out to be apparently state-dependent, decreasing the torpor response in relatively heavy individuals, whilst relatively light individuals were unaffected. Consistent with our results, higher barometric pressure may be used by the bats as a proxy for good foraging conditions, leading to increased activity levels (Wolcott and Vulinec 2012; Bender and Hartman 2015), while falling barometric pressures have been shown to increase activity level in insectivorous bats, which has been linked to an increase in insect abundance (Paige 1995; Turbill 2008). However, our 24-h change in barometric pressure variable should perhaps be interpreted with caution, because the within-subjects effect was positive in the best within-subjects model when included alongside all the other effects (Fig. 4e), but negative in the simple models comparing amount- and within-subjects effect together in the same models that included temperature and only one other variable at the time (Fig. 5e). This indicates that, despite our efforts to control for covariance issues between our explanatory variables during our analyses, the effect shifts in this variable depending on whether it is modelled with other variables or only with T_a, suggesting a complex series of interactions between environmental effects.

Increased relative humidity was found to lengthen nightly torpor duration in the eastern long-eared bats, independent of sex or individual state, and appeared as the second strongest predictor in the best within-subject effect model. Studies investigating nightly bat activity, however, report contradictory results, showing both greater bat activity with increasing relative humidity (Lacki 1984; Wolcott and Vulinec 2012) and lower bat activity with increasing relative humidity (O’Farrell and Bradley 1970). As we have analyzed data throughout seasons and locations, the overall and rather strong within-subjects humidity effect on nightly torpor use indicates that humidity conditions may be a more important driver of torpor use than previously reported, probably due to its negative effect on prey availability.

A topic that has caught the attention of many bat researchers is the effect of moonlight and/or lunar phase on bat activity. Here, we report a positive relationship between moon disk illumination and nightly torpor use in eastern long-eared bats. Many studies have previously investigated this effect and the results have been mixed, involving both negative effects of moonlight on bat activity and/or shifts to darker foraging habitats (Fenton et al. 1977; Lang et al. 2006; Appel et al. 2017), positive effects of moonlight on bat activity (Erickson and West 2002; Appel et al. 2017), or no effect at all (Karlsson et al. 2002; Holland et al. 2011). Some studies also point out shifts in insect abundance with lunar phases as a source of variation in the nightly activity patterns of insectivorous bats (Yela and Holyoak 1997; Lang et al. 2006). The variability and complexity of such moonlight effects on foraging success and/or predation risk suggests that this is likely to be highly species and habitat dependent. A review on anti-predator behaviour in bats by Lima and O'Keefe (2013), and the meta-analysis study on moonlight-avoidance by Saldaña-Vázquez and Munguía-Rosas (2013), both suggest that apparent 'lunar phobia' occurs mainly in tropical bat species. For temperate zone studies, there is little support for moonlight aversion in bats (Lima and O'Keefe 2013), and latitude was estimated to have a slight positive effect on lunar phobia across bat species (Saldaña-Vázquez and Munguía-Rosas 2013). The bats in our study, in both tropical and subtropical locations, showed a lunar phobic response by increasing their torpor use on nights with higher levels of moon disk illumination. This effect was surprisingly strong, comparable with other weather variables (excluding temperature and humidity), especially given that the variable did not account for potential variability in illumination due to cloud cover (see "Methods"). As other weather variables that may affect prey availability are accounted for in the analyses, our results show moon phases to be an important factor in individual bat nightly foraging decisions and energy budgeting across seasons and locations, potentially due to increased perceived predation risk under greater night-time illumination.

In this study, we have shown that across seasons and locations eastern long-eared bats in Australia employ torpor during the night as a consistent and predictable response to weather conditions and individual state. It appears that multiple environmental factors, as well as individual state (e.g. relative body mass, torpor the night before), are together taken into account in the use of night-time torpor versus active foraging or roosting. This species is endemic to the subtropical and tropical regions of Australia and faces a rapidly changing environment consistent with global trends. Many species have already shown responses to a changing climate by changing their distributional ranges, altering migration patterns or changing the timing of seasonal activities, potentially resulting in mismatching phenologies (IPCC 2014). However, temporal heterotherms may be buffered against certain costs of a changing climate by being more able to adjust their energy requirements through torpor and hibernation depending upon season and/or latitude. These are strategies that have been identified as key factors in reducing extinction risk in mammal species (Geiser and Turbill 2009; Liow et al. 2009). Hence, studies investigating the effect of climatic changes on long-term population trends in Europe found either weak or inconclusive effects on bat populations (Bowler et al. 2015; Martay et al. 2017). At the same time, bat populations are declining across a range of different species and environments, likely due to the cumulative effects of habitat loss, climate change, anthropogenic stressors and diseases (Rodhouse et al. 2012; Frick et al. 2019). Our results show how one bat species appears to strategically balance its energy budget by altering night-time torpor use when faced with varying weather conditions and individual state. In light of such phenotypic plasticity, it is currently unclear how much eastern long-eared bat populations and their distribution ranges will be affected by the predicted long-term increases in temperatures, droughts and shifts in atmospheric circulation on the east coast of Australia (Murphy and Timbal 2008). However, our results highlight the complexity and importance of weather conditions on insectivorous bat energy budgets, suggesting that the ongoing environmental change may have considerable impacts on the individual torpor and hibernation patterns across seasons and locations.

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Author contribution statement CS and JW designed the study; CS conducted the fieldwork and collected the data; MAF performed analyses and interpretation with input from CS and JW; MAF led the writing of the manuscript, which was commented on and revised by CS and JW. All authors gave their final approval for publication and agreed to be accountable for all aspects of the study.

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Data availability The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional and national guidelines for the care and use of animals were followed (see "Methods" for permit information).

Consent to participate Not applicable.

Consent for publication Not applicable.

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Supplementary Materials 1: Correlation matrices

Table S1.1: Correlation matrix for the mean nightly variables. The number of asterisks indicate when p-values are < 0.5 (*), < 0.01 (**) and < 0.001 (***).

	Ta_{Mean}	$Rain_{Mean}$	$Wind_{Mean}$	$Humid_{Mean}$	BP_{Mean}	ΔBP
Ta_{Mean}	1					
$Rain_{Mean}$	0.32 ***	1				
$Wind_{Mean}$	0.09	0.43 ***	1			
$Humid_{Mean}$	0.54 ***	0.24 ***	-0.34 ***	1		
BP_{Mean}	-0.18 **	-0.29 ***	-0.34 ***	0.21 ***	1	
ΔBP	-0.14 *	-0.34 ***	-0.11	-0.30 ***	0.33 ***	1
Moon	-0.01	0.01	0.01	0.07	-0.16 *	-0.12 *

Table S1.2: Correlation matrix for the range nightly variables.

	Ta_{Range}	$Rain_{Range}$	$Wind_{Range}$	$Humid_{Range}$	BP_{Range}
Ta_{Range}	1				
$Rain_{Range}$	-0.43 ***	1			
$Wind_{Range}$	-0.12 *	0.19 **	1		
$Humid_{Range}$	0.35 ***	-0.15 *	0.06	1	
BP_{Range}	-0.01	0.21 ***	0.22 ***	0.18 **	1

Table S1.3: Correlation matrix between the mean versus range nightly variables.

	Ta_{Mean}	$Rain_{Mean}$	$Wind_{Mean}$	$Humid_{Mean}$	BP_{Mean}
Ta_{Range}	-0.69 ***	-0.38 ***	0.03	-0.51 ***	-0.07
$Rain_{Range}$	0.36 ***	0.89 ***	0.25 ***	0.27 ***	-0.17 **
$Wind_{Range}$	0.38 ***	0.20 ***	0.39 ***	-0.05	-0.34 ***
$Humid_{Range}$	-0.19 **	-0.22 ***	-0.09	-0.08	0.01
BP_{Range}	0.25 ***	0.27 ***	0.32 ***	0.03	-0.53 ***

Supplementary Materials 2: Model selection

Original Global Model:

The global original model was constructed with interaction effects between each parameter, which included sex, each of the mean environmental variables (T_a, precipitation, wind speed, humidity and barometric pressure), ΔBP and moon disk illumination. Individual ID and date ID were included as random effects. The results from the global model are shown in Table S2.1, while Table S2.2 shows the 10 highest ranked models after performing the model selection.

Table S2.1: Estimates, standard error and p-values of each variable included in the global model using the original variables, where the numerical predictors are scaled for comparison of their effect on nightly torpor duration in eastern long-eared bats. p-values for males (♂) for each environmental variable indicate whether the effect was significantly different from females (♀). Day and individual ID were fitted as random effects and are given as the proportion of total variation explained.

Variable	Estimate	Std. Error	p-value
Random effects			
Day ID	0.02	0.0005	
Individual ID	0.05	0.0008	
Residual	0.07	0.001	
Fixed effects			
Intercept ♀	480.2	42.2	< 0.001
Intercept ♂	416.4	27.6	< 0.05
T_a ♀	-291.4	33.2	< 0.001
T_a ♂	-314.4	23.3	0.33
Humidity ♀	49.6	24.3	< 0.05
Humidity ♂	68.5	18.4	0.31
BP ♀	-42.8	16.8	< 0.05
BP ♂	-68.8	15.2	0.09
ΔBP ♀	16.7	14.8	0.26
ΔBP ♂	28.9	13.6	0.37
Wind speed ♀	23.1	21.6	0.29
Wind speed ♂	21.0	19.3	0.91
Moon size ♀	17.3	16.2	0.29
Moon size ♂	33.0	15.8	0.32
Precipitation ♀	140.0	111.2	0.21
Precipitation ♂	175.0	15.4	< 0.05
T_a : Humidity	11.5	15.2	0.45
T_a : BP	17.6	10.9	0.11
T_a : ΔBP	-30.3	11.6	< 0.05
T_a : Wind speed	-2.1	19.3	0.91
T_a : Moon size	15.8	13.9	0.26
T_a : Precipitation	-68.2	89.4	0.45
Humidity : BP	19.6	14.4	0.18
Humidity : ΔBP	24.8	18.6	0.19
Humidity : Wind speed	-21.2	14.7	0.15
Humidity : Moon size	39.8	17.2	< 0.05

Humidity : Precipitation	-75.5	56.5	0.18
BP : ΔBP	-5.1	13.4	0.70
BP : Wind speed	12.6	17.3	0.47
BP : Moon size	-19.8	11.6	0.09
BP : Precipitation	-1.3	37.6	0.97
ΔBP : Wind speed	38.0	19.8	0.06
ΔBP : Moon size	26.2	10.8	< 0.05
ΔBP : Precipitation	-38.3	31.5	0.23
Wind speed : Moon size	-6.9	14.0	0.62
Wind speed : Precipitation	11.8	41.2	0.77
Moon size : Precipitation	-36.6	35.4	0.30

Table S2.2: The 10 highest ranked models derived from the model selection based on the original global model:

Rank	Model	Max. VIF	df	AIC	ΔAIC
1	Torpor ~ Ta*ΔBP + Sex*Rain + Moon*(Rain + BP + Humidity + ΔBP) + Humidity*(Wind + BP)	2.5	20	3278.14	0.0
2	Torpor ~ Ta*(Moon + ΔBP) + Sex*Rain + Moon*(Rain + BP + Humidity + ΔBP) + Humidity*(Wind + BP)	2.5	21	3278.98	0.8
3	Torpor ~ Ta*(Moon + ΔBP) + Sex*(Rain + Moon) + Moon*(Rain + BP + Humidity + ΔBP) + Humidity*(Wind + BP)	2.5	22	3279.41	1.3
4	Torpor ~ Ta*(BP + Moon + ΔBP) + Sex*(Rain + Moon) + Moon*(Rain + BP + Humidity + ΔBP) + Humidity*(Wind + BP)	2.9	23	3279.71	1.6
5	Torpor ~ Ta*(BP + Moon + ΔBP) + Sex*(BP + Rain + Moon) + Moon*(Rain + BP + Humidity + ΔBP) + Humidity*(Wind + BP)	2.9	24	3280.63	2.5
6	Torpor ~ Ta*(Sex + BP + Moon + ΔBP) + Sex*(BP + Rain + Moon) + Moon*(Rain + BP + Humidity + ΔBP) + Humidity*(Wind + BP)	2.9	25	3282.17	4.0
7	Torpor ~ Ta*(Sex + BP + Moon + ΔBP) + Sex*(BP + Rain + Moon) + Moon*(Rain + BP + Humidity + ΔBP + Wind) + Humidity*(Wind + BP)	3.5	26	3283.59	5.5
8	Torpor ~ Ta*(Sex + BP + Moon + ΔBP) + Sex*(Humidity + BP + Rain + Moon) + Moon*(Rain + BP + Humidity + ΔBP + Wind) + Humidity*(Wind + BP) + Wind*ΔBP	6.1	28	3285.02	6.9
9	Torpor ~ Ta*(Sex + BP + Moon + ΔBP) + Sex*(Humidity + BP + Rain + Moon) + Moon*(Rain + BP + Humidity + ΔBP + Wind) + Humidity*(Wind + BP)	3.6	27	3285.20	7.1
10	Torpor ~ Ta*(Humidity + Sex + BP + Moon + ΔBP) + Sex*(Humidity + BP + Rain + Moon) + Moon*(Rain + BP + Humidity + ΔBP + Wind) + Humidity*(Wind + BP) + Wind*ΔBP	6.1	29	3286.52	8.4

Within-Subjects Model:

The global within-subjects model using individually mean-centred variables was constructed in the same way as the global model using the original variables, with interaction terms between each fixed effect. Day ID was included as random effect. The results from the within-subjects model are shown in Table S2.3, while Table S2.4 shows the 10 highest ranked models after performing the model selection.

Table S2.3: Estimates, standard error and p-values of each variable included in the global within subjects model using individually mean-centred variables, where the numerical predictors are scaled for comparison of their effect on nightly torpor duration. p-values for males (♂) for each environmental variable indicate whether the effect was significantly different from females (♀).

Variable	Estimate	Std. Error	p-value
Random effects			
Day ID	0.07	0.002	
Residual	0.30	0.004	
Fixed effects			
Intercept ♀	5.4	10.0	0.59
Intercept ♂	-2.8	10.1	0.42
T_a ♀	-283.0	24.4	< 0.001
T_a ♂	-281.5	31.1	0.96
Humidity ♀	72.6	15.7	< 0.001
Humidity ♂	70.4	19.5	0.91
BP ♀	-29.9	13.0	< 0.05
BP ♂	-50.7	16.6	0.21
ΔBP ♀	17.9	11.1	0.11
ΔBP ♂	24.0	14.2	0.67
Wind speed ♀	38.4	18.4	< 0.05
Wind speed ♂	28.9	22.2	0.67
Moon size ♀	42.5	14.2	< 0.01
Moon size ♂	38.4	16.9	0.81
Precipitation ♀	26.3	14.1	0.06
Precipitation ♂	57.2	17.1	0.07
T_a : Humidity	-8.1	27.9	0.77
T_a : BP	92.7	35.9	< 0.05
T_a : ΔBP	-66.7	41.8	0.11
T_a : Wind speed	48.8	43.4	0.26
T_a : Moon size	55.0	34.6	0.11
T_a : Precipitation	-81.7	39.9	< 0.05
Humidity : BP	-21.4	14.9	0.16
Humidity : ΔBP	9.4	20.1	0.64
Humidity : Wind speed	25.9	29.3	0.38
Humidity : Moon size	24.6	20.4	0.23
Humidity : Precipitation	-25.2	44.6	0.57
BP : ΔBP	-6.5	13.2	0.62
BP : Wind speed	7.2	19.2	0.71
BP : Moon size	-24.1	22.0	0.28
BP : Precipitation	9.7	29.9	0.75
ΔBP : Wind speed	5.7	23.4	0.81

ΔBP : Moon size	37.4	14.7	< 0.05
ΔBP : Precipitation	-34.4	20.1	0.09
Wind speed : Moon size	28.4	25.0	0.26
Wind speed : Precipitation	-28.4	20.8	0.17
Moon size : Precipitation	-2.8	20.8	0.89

Table S2.4: The 10 highest ranked models derived from the model selection based on the within-subjects global model. The best model was selected based on AIC ranking and the lowest degrees of freedom as there were several models with AIC-values < 2 points from the best model:

Rank	Model	Max. VIF	df	AIC	ΔAIC
1	Torpor ~ Ta + Sex*Rain + Wind + BP + ΔBP + Humid + Moon	1.8	12	3199.45	0.0
2	Torpor ~ Ta*(Rain + Moon + BP) + Sex*Rain + Moon*(Wind + ΔBP + BP) + Humid	2.1	19	3198.88	-0.6
3	Torpor ~ Ta*Rain + Sex*Rain + Wind + BP + ΔBP + Humid + Moon	2	13	3198.99	-0.5
4	Torpor ~ Ta*(Rain + Moon + BP) + Sex*Rain + Moon*(Wind + ΔBP + BP) + Humid	2.1	18	3199.08	-0.4
5	Torpor ~ Ta*(Rain + Moon) + Sex*Rain + Wind + BP + ΔBP + Humid + Moon	2	14	3199.30	-0.1
6	Torpor ~ Ta*(Rain + Moon) + Sex*Rain + Moon*(Wind + ΔBP) + BP + Humid	2	16	3199.35	-0.1
7	Torpor ~ Ta*(Rain + Moon) + Sex*Rain + Moon*Wind + BP + ΔBP + Humid	2	15	3199.51	0.1
8	Torpor ~ Ta*(Rain + Moon + BP + Wind) + Sex*(Rain + BP) + Moon*(Wind + ΔBP + BP + Humid)	2.3	22	3199.71	0.3
9	Torpor ~ Ta*(Rain + Moon + BP) + Sex*Rain + Moon*(Wind + ΔBP) + Humid	2.1	17	3199.74	0.3
10	Torpor ~ Ta*(Rain + Moon + BP + Wind) + Sex*Rain + Moon*(Wind + ΔBP + BP + Humid)	2.3	21	3199.74	0.3

Original Model Including State Variables:

The global model using the original variables is presented here but with sex being replaced by forearm length and body mass (see Methods regarding covariance issues here), and including interaction terms between the two state-variables and each of the environmental variables, as well as three-way interaction terms between each of the state variables and the identified two-way interactions from the best original model (rank 1, Table S2.2). The results from the global model are shown in Table S2.5, while Table S2.6 shows the 10 highest ranked models after performing the model selection.

Table S2.5: Estimates, standard error and p-values of each variable included in the global model using the original explanatory variables, where the numerical predictors are scaled for comparison of their effect on nightly torpor duration.

Variable	Estimate	Std. Error	p-value
Random effects			
Day ID	0.03	0.0006	
Individual ID	0.05	0.0008	
Residual	0.05	0.0008	
Fixed effects			
Intercept	415.3	19.1	< 0.001
T_a	-276.2	17.6	< 0.001
Humidity	43.0	18.7	< 0.05
BP	-32.4	14.1	< 0.05
ΔBP	19.0	13.7	0.17
Wind speed	21.8	15.2	0.15
Moon size	34.4	14.6	< 0.05
Precipitation	65.0	13.9	< 0.001
Forearm length (FA)	23.4	18.5	0.22
Body mass (BM)	19.1	22.5	0.40
BM : Ta	2.1	24.2	0.93
BM : Humid	3.4	21.3	0.87
BM : BP	-4.9	14.5	0.73
BM : ΔBP	11.5	10.9	0.29
BM : Wind	20.2	16.3	0.22
BM : Moon	15.5	17.2	0.37
BM : Precipitation	43.8	23.8	0.07
FA : Ta	11.8	16.3	0.47
FA : Humid	12.3	13.8	0.37
FA : BP	8.2	12.6	0.52
FA : ΔBP	-4.2	9.4	0.66
FA : Wind	4.0	12.0	0.74
FA : Moon	-11.0	11.4	0.34
FA : Precipitation	-38.9	11.5	< 0.001
T_a : ΔBP	-15.6	11.7	0.18
Moon : Precipitation	-53.8	19.1	< 0.01
Moon : BP	-29.1	13.9	< 0.05
Moon : Humid	50.5	15.3	< 0.01
Moon : ΔBP	36.9	15.6	< 0.05
Humidity : Wind	-35.5	15.1	< 0.05

Humidity : BP	32.2	18.1	0.08
Ta : ΔBP : BM	-3.2	11.7	0.78
Moon : Precipitation : BM	51.1	41.0	0.22
Moon : BP : BM	-49.7	17.6	< 0.01
Moon : Humid : BM	28.4	23.7	0.23
Moon : ΔBP : BM	25.7	17.1	0.14
Humidity : Wind : BM	-2.6	20.9	0.90
Humidity : BP : BM	0.1	15.2	0.99
Ta : ΔBP : FA	-9.0	9.1	0.32
Moon : Precipitation : FA	-0.4	15.7	0.98
Moon : BP : FA	18.9	15.5	0.23
Moon : Humid : FA	-22.2	12.2	0.07
Moon : ΔBP : FA	-31.0	13.7	< 0.05
Humidity : Wind : FA	5.4	11.9	0.65
Humidity : BP : FA	10.1	14.4	0.48

Table S2.6: The 10 highest ranked models derived from the model selection based on the global model. The best model was selected based on AIC ranking and the lowest degrees of freedom as there were several models with AIC-values < 2 points from the best model (the second ranked model had an AIC-value > 2 points from the best model, but was ranked second based on the degrees of freedom and the significance-level of the removed parameters, which were non-significant):

Rank	Model	Max. VIF	df	AIC	ΔAIC
1	Torpor ~ Ta*DBP + Moon*(Humid + Rain) + Humid*(BP + Wind) + FA*Rain + BM*Wind	2.2	20	2610.22	0.0
2	Torpor ~ Ta*DBP + Moon*(Humid + Rain) + Humid*(BP + Wind) + FA*(Rain + BP) + BM*(Wind + BP)	2.2	22	2608.16	-2.1
3	Torpor ~ Ta*DBP + Moon*(Humid + Rain + ΔBP) + Humid*(BP + Wind) + FA*(Rain + BP) + BM*(Wind + BP)	2.2	23	2609.09	-1.1
4	Torpor ~ Ta*DBP + Moon*(Humid + Rain + ΔBP) + Humid*(BP + Wind) + FA*(Rain + BP + ΔBP) + BM*(Wind + BP + ΔBP)	2.2	25	2609.16	-1.1
5	Torpor ~ Ta*DBP + Moon*(Humid + Rain + ΔBP + BP) + Humid*(BP + Wind) + FA*(Rain + BP + ΔBP + Moon) + BM*(Wind + BP + ΔBP)	2.5	27	2609.16	-1.1
6	Torpor ~ Ta*DBP + Moon*(Humid + Rain + ΔBP + BP) + Humid*(BP + Wind) + FA*(Rain + BP + ΔBP) + BM*(Wind + BP + ΔBP)	2.5	26	2609.29	-0.9
7	Torpor ~ Ta*DBP + Moon*(Humid + Rain + ΔBP) + Humid*(BP + Wind) + FA*(Rain + BP) + BM*(Wind + BP + ΔBP)	2.2	24	2609.35	-0.9
8	Torpor ~ Ta*DBP + Moon*(Humid + Rain) + Humid*(BP + Wind) + FA*(Rain + BP) + BM*(Wind)	2.2	21	2529.79	-0.5
9	Torpor ~ Ta*DBP + Moon*(Humid + Rain + ΔBP + BP) + Humid*(BP + Wind) + FA*(Rain + BP + ΔBP + Moon) + BM*(Wind + BP + ΔBP + Moon)	2.5	28	2610.04	-0.2
10	Torpor ~ Ta*DBP + Moon*(Humid + Rain + ΔBP + BP) + Humid*(BP + Wind) + FA*(Rain + BP + ΔBP + Moon) + BM*(Wind + BP + ΔBP + Moon + Rain)	2.7	29	2610.96	0.7

Within-subject model with state variables:

The global within-subjects model using individually mean-centred explanatory variables is presented here with forearm length and body mass replacing sex (see Methods regarding covariance issues here), it included interaction terms between the two state-variables and each of the environmental variables. The results from the global model are shown in Table S2.7, while Table S2.8 shows the 10 highest ranked models after performing the model selection.

Table S2.7: Estimates, standard error and p-values of each variable included in the within-subjects global model using individually mean-centred explanatory variables, with body mass and fore-arm length in place of sex, where the numerical predictors are scaled for comparison of their effect on nightly torpor duration.

Variable	Estimate	Std. Error	p-value
	Random effects		
Day ID	0.13	0.002	
Residual	0.20	0.003	
	Fixed effects		
Intercept	-5.2	7.9	0.51
T_a	-314.4	22.0	< 0.001
Humidity	65.6	15.7	< 0.001
BP	-34.7	13.1	< 0.01
ΔBP	22.0	11.4	0.06
Wind speed	45.4	16.3	< 0.01
Moon size	58.3	11.8	< 0.001
Precipitation	38.1	11.3	< 0.01
Forearm length (FA)	2.7	5.5	0.62
Body mass (BM)	0.6	8.5	0.95
BM : Ta	-36.6	33.4	0.28
BM : Humid	1.1	19.5	0.96
BM : BP	-12.4	14.7	0.40
BM : ΔBP	23.4	11.2	< 0.05
BM : Wind	53.5	19.8	< 0.01
BM : Moon	16.9	22.3	0.45
BM : Precipitation	24.5	18.2	0.18
FA : Ta	36.1	17.0	< 0.05
FA : Humid	-0.4	11.4	0.97
FA : BP	17.4	9.9	0.08
FA : ΔBP	-6.9	8.8	0.43
FA : Wind	-17.1	11.4	0.14
FA : Moon	-17.1	8.9	0.06
FA : Precipitation	-25.4	7.6	< 0.01

Table S2.8: The 10 highest ranked models derived from the model selection based on the global within-subjects model. The best model was selected based on AIC ranking and the lowest degrees of freedom as there were several models with AIC-values < 2 points from the best model:

Rank	Model	Max. VIF	df	AIC	ΔAIC
1	Torpor ~ BM*(Rain + Wind + DBP) + FA*Rain + Ta + BP + Humid + Moon	3.2	16	2470.73	0.0
2	Torpor ~ BM*(Rain + Wind + DBP) + FA*(Ta + Rain + Moon) + BP + Humid	3.2	18	2469.02	-1.7
3	Torpor ~ BM*(Rain + Wind + DBP) + FA*(Rain + Moon) + Ta + BP + Humid	3.2	17	2469.52	-1.2
4	Torpor ~ BM*(Rain + Wind + DBP) + FA*(Ta + Rain + Moon + BP) + Humid	3.2	19	2469.67	-1.1
5	Torpor ~ BM*(Ta + Rain + Wind + DBP + BP) + FA*(Ta + Rain + Moon + Wind + BP) + Humid	3.7	22	2469.90	-0.8
6	Torpor ~ BM*(Ta + Rain + Wind + DBP) + FA*(Ta + Rain + Moon + BP) + Humid	3.4	20	2469.90	-0.8
7	Torpor ~ BM*(Ta + Rain + Wind + DBP + BP) + FA*(Ta + Rain + Moon + BP) + Humid	3.6	21	2469.94	-0.8
8	Torpor ~ BM*(Ta + Rain + Moon + Wind + DBP + BP) + FA*(Ta + Rain + Moon + Wind + BP) + Humid	4.0	23	2471.53	0.8
9	Torpor ~ BM*(Ta + Rain + Moon + Wind + DBP + BP) + FA*(Ta + Rain + Moon + Wind + DBP + BP) + Humid	4.0	24	2472.78	2.0
10	Torpor ~ BM*(Rain + DBP) + FA*Rain + Ta + BP + Humid + Moon	2.1	15	2472.90	2.2

Supplementary Material 3: Interaction effects from original model

The best global model using the original explanatory variables included 7 different interaction terms between the various environmental variables. These included interactions between moon size and 4 other variables (humidity, barometric pressure, ΔBP and precipitation), in addition to interactions between T_a and ΔBP, between humidity and wind, and between humidity and barometric pressure. See Table 1 in Results for effect-values, and Fig. S3.1 for the visualized interaction effects made by predicting the effect and confidence intervals across the observed predictor-range, using the delta-method. However, these interaction effects all disappeared from the best model when performing the model selection for the within-subject effects, indicating that they are likely to be caused by differences in environmental conditions measured for the different individuals (i.e. among-subject effects), and they should therefore be interpreted with caution.

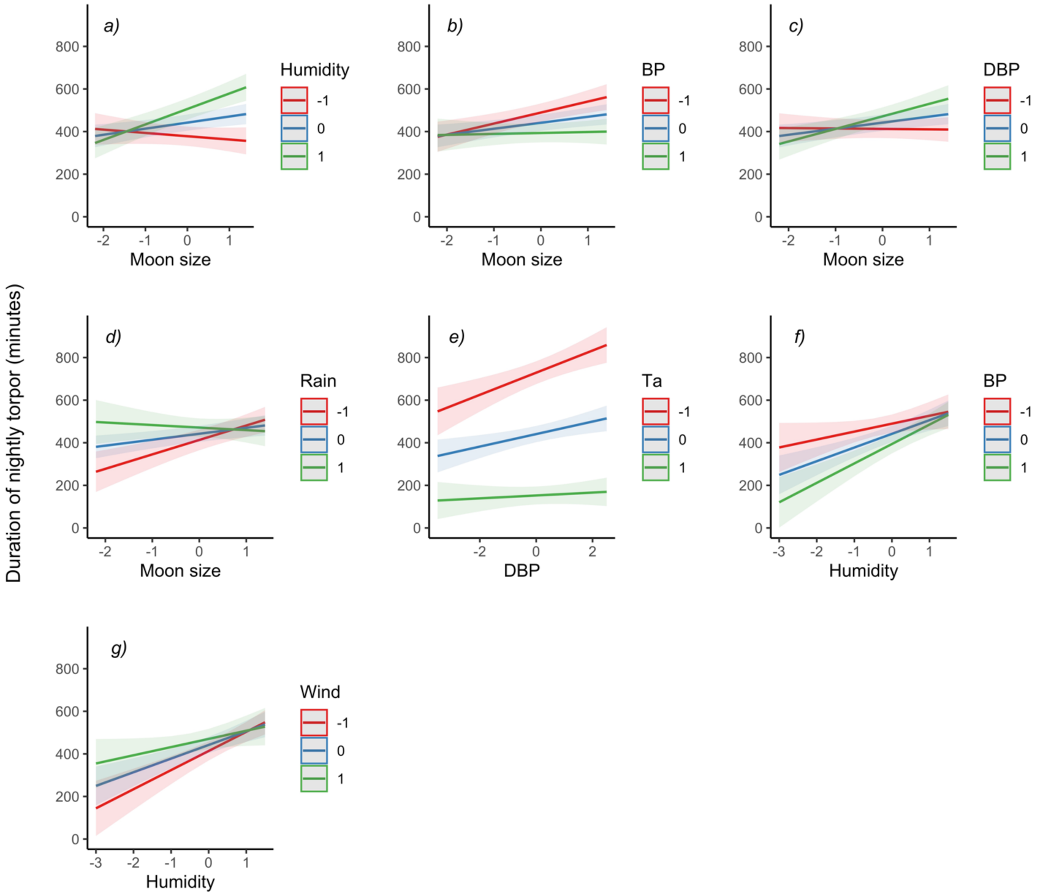

Figure S3.1: Interaction effects from the best global model for the different original explanatory variables. The colours correspond to the values 0 (blue), 1 (green), or -1 (red) for the scaled predictors explaining the effects. We chose to focus on the variables in the interaction which we believed to be the most novel or interesting when presenting each interaction-effect.

Supplementary Material 4: Within- vs. Among-Subject Effects

Due to convergence issues with the larger models when attempting to disentangle within- and among-subject effects (see Methods), we investigated these effects through the 7 simple models that are presented below. The models tested effects of one environmental variable at the time while accounting for the effects of T_a, as this was the strongest predictor of nightly torpor use. To disentangle the within- vs. among-subject effects we followed the 3 steps described in van de Pol & Wright (2009).

Model 1: Torpor ~ T_a
Model 2: Torpor ~ T_a + Precipitation
Model 3: Torpor ~ T_a + Wind
Model 4: Torpor ~ T_a + BP
Model 5: Torpor ~ T_a + ΔBP
Model 6: Torpor ~ T_a + Humidity
Model 7: Torpor ~ T_a + Moon size

Model results are shown in the Tables S4.1 to S4.7 with values for each of the three steps presented (original; within subjects (W); among subjects (A)). Black values indicate significant effects ($p < 0.05$), while red values are non-significant. The results show that the strongest predictor, T_a, has a consistent effect in all the models (overall effect ranging from -253.0 to -271.3), which suggests that no interaction effects are causing major issues with this predictor. Further, the results show a non-significant difference between within- and among-subject effects for all the environmental effects except for precipitation, where the among-subject effect was stronger than the within-subject effect, although both showed significant effects in themselves. This indicates that part of the precipitation effect found in the original model is caused by among-subject effects.

Table S4.1: Model results from model 1 for the three models (step 1-3) tested in order to disentangle within- and among-subject effects. Standard deviation (random effects) and standard error (fixed effects) are shown in parentheses. Day and individual ID were fitted as random effects and are given as the proportion of total variation explained. Black values are significant ($p < 0.05$), while red values are non-significant.

Model 1: Torpor ~ T_a			
	Step 1 (original)	**Step 2 (W. & A.)**	**Step 3 (W. vs. A)**
	Random effects		
Day ID	0.09 (±0.001)	0.09 (±0.001)	0.09 (±0.001)
Individual ID	0.08 (±0.0009)	0.07 (±0.0009)	0.07 (±0.0009)
Residual	0.08 (±0.001)	0.08 (±0.0009)	0.08 (±0.0009)
	Fixed effects		
Intercept	411.1 (±18.7)	417.7 (±19.0)	417.7 (±19.0)
T_a	-253.0 (±16.0)		
T_a(W)		-226.9 (±25.4)	-226.9 (±25.4)
T_a(A)		-269.3 (±19.8)	
T_a(A-W)			-42.4 (±32.0)

Table S4.2: Model results from model 2 for the three models (step 1-3) tested in order to disentangle within- and among-subject effects.

Model 2: Torpor ~ T_a + Precipitation			
	Step 1 (original)	**Step 2 (W. & A.)**	**Step 3 (W. vs. A)**
	Random effects		
Day ID	0.07 (±0.001)	0.07 (±0.0009)	0.07 (±0.0009)
Individual ID	0.08 (±0.001)	0.06 (±0.0008)	0.06 (±0.0008)
Residual	0.09 (±0.001)	0.08 (±0.001)	0.08 (±0.001)
	Fixed effects		
Intercept	416.6 (±18.0)	425.5 (±17.5)	425.5 (±17.5)
T_a	-261.6 (±5.2)		
T_a(W)		-235.3 (±23.1)	-235.3 (±23.1)
T_a(A)		-294.3 (±19.5)	
T_a(A-W)			-59.0 (±29.8)
Rain	50.7 (±12.9)		
Rain (W)		44.6 (±12.8)	44.6 (±12.9)
Rain (A)		91.7 (±21.4)	
Rain (A-W)			47.1 (±20.4)

Table S4.3: Model results from model 3 for the three models (step 1-3) tested in order to disentangle within- and among-subject effects.

Model 3: Torpor ~ T_a + Wind			
	Step 1 (original)	**Step 2 (W. & A.)**	**Step 3 (W. vs. A)**
Random effects			
Day ID	0.09 (±0.001)	0.08 (±0.0009)	0.08 (±0.0009)
Individual ID	0.08 (±0.0009)	0.07 (±0.0009)	0.07 (±0.0009)
Residual	0.08 (±0.001)	0.08 (±0.0009)	0.08 (±0.0009)
Fixed effects			
Intercept	413.1 (±18.8)	419.2 (±19.1)	419.2 (±19.1)
T_a	-256.0 (±16.0)		
T_a(W)		-231.4 (±25.4)	-231.4 (±25.5)
T_a(A)		-271.7 (±20.1)	
T_a(A-W)			-40.3 (±32.2)
Wind	22.4 (±13.9)		
Wind (W)		15.1 (±18.2)	15.1 (±18.2)
Wind (A)		26.5 (±18.0)	
Wind (A-W)			11.3 (±23.2)

Table S4.4: Model results from model 4 for the three models (step 1-3) tested in order to disentangle within- and among-subject effects.

Model 4: Torpor ~ T_a + BP			
	Step 1 (original)	**Step 2 (W. & A.)**	**Step 3 (W. vs. A)**
Random effects			
Day ID	0.08 (±0.0009)	0.07 (±0.0009)	0.07 (±0.0009)
Individual ID	0.07 (±0.0009)	0.07 (±0.0008)	0.07 (±0.0008)
Residual	0.08 (±0.0009)	0.07 (±0.0009)	0.07 (±0.0009)
Fixed effects			
Intercept	416.1 (±18.4)	423.2 (±18.8)	423.2 (±18.8)
T_a	-263.2 (±15.9)		
T_a(W)		-236.2 (±24.5)	-236.2 (±24.5)
T_a(A)		-284.6 (±20.5)	
T_a(A-W)			-48.3 (±31.7)
BP	-38.3 (±12.4)		
BP (W)		-32.0 (±14.0)	-32.0 (±14.0)
BP (A)		-54.4 (±21.5)	
BP (A-W)			-22.4 (±24.4)

Table S4.5: Model results from model 5 for the three models (step 1-3) tested in order to disentangle within- and among-subject effects.

Model 5: Torpor ~ T_a + ΔBP			
	Step 1 (original)	**Step 2 (W. & A.)**	**Step 3 (W. vs. A)**
	Random effects		
Day ID	0.09 (±0.001)	0.08 (±0.0009)	0.08 (±0.0009)
Individual ID	0.08 (±0.0009)	0.07 (±0.0009)	0.07 (±0.0009)
Residual	0.08 (±0.001)	0.07 (±0.0009)	0.07 (±0.0009)
	Fixed effects		
Intercept	410.9 (±18.8)	416.2 (±19.2)	416.2 (±19.2)
T_a	-255.4 (±16.2)		
T_a(W)		-229.1 (±25.9)	-229.1 (±25.9)
T_a(A)		-273.4 (±20.4)	
T_a(A-W)			-44.3 (±32.9)
ΔBP	-19.5 (±11.9)		
ΔBP (W)		-15.1 (±12.4)	-15.1 (±12.4)
ΔBP (A)		-35.5(±27.6)	
ΔBP (A-W)			-20.4 (±28.0)

Table S4.6: Model results from model 6 for the three models (step 1-3) tested in order to disentangle within- and among-subject effects.

Model 6: Torpor ~ T_a + Humidity			
	Step 1 (original)	**Step 2 (W. & A.)**	**Step 3 (W. vs. A)**
	Random effects		
Day ID	0.08 (±0.001)	0.08 (±0.0009)	0.08 (±0.0009)
Individual ID	0.09 (±0.001)	0.08 (±0.0009)	0.08 (±0.0009)
Residual	0.08 (±0.001)	0.08 (±0.0009)	0.08 (±0.0009)
	Fixed effects		
Intercept	413.1 (±19.1)	419.2 (±19.4)	419.2 (±19.4)
T_a	-271.3 (±17.3)		
T_a(W)		-254.9 (±26.0)	-254.9 (±26.0)
T_a(A)		-275.5 (±24.0)	
T_a(A-W)			-20.6 (±35.2)
Humid	44.4 (±15.0)		
Humid (W)		47.6 (±16.4)	47.6 (±16.4)
Humid (A)		20.7 (±32.4)	
Humid (A-W)			-26.9 (±35.3)

Table S4.7: Model results from model 7 for the three models (step 1-3) tested in order to disentangle within- and among-subject effects.

Model 7: Torpor ~ T_a + Moon			
	Step 1 (original)	**Step 2 (W. & A.)**	**Step 3 (W. vs. A)**
	Random effects		
Day ID	0.08 (±0.0009)	0.08 (±0.0009)	0.08 (±0.0009)
Individual ID	0.06 (±0.0009)	0.06 (±0.0008)	0.06 (±0.0008)
Residual	0.08 (±0.0009)	0.07 (±0.0009)	0.07 (±0.0009)
	Fixed effects		
Intercept	423.5 (±17.9)	425.3 (±18.3)	425.3 (±18.3)
T_a	-258.5 (±15.2)		
T_a(W)		-247.8 (±25.2)	-247.8 (±25.2)
T_a(A)		-266.6 (±19.1)	
T_a(A-W)			-18.8 (±31.2)
Moon	45.9 (±11.5)		
Moon (W)		46.9 (±13.4)	46.9 (±13.4)
Moon (A)		39.4 (±18.1)	
Moon (A-W)			-7.5 (±20.3)

Supplementary Material 5: State Dependence

Body Mass and Forearm Length

As forearm length and body mass were not significantly correlated (0.31, p = 0.07) they could both be included in the models when performing the model selection. However, correlation issues emerged when including forearm and body mass together with sex in the models, as females in this species and sample have significantly larger forearms (1.34 ± 0.44, $p < 0.01$) and are significantly heavier (1.96 ± 0.34, $p < 0.001$) than males. In order to investigate state dependency on nightly torpor employed by eastern long-eared bats we replaced body mass and forearm length with sex and performed a model selection based on a global original model and a global within-subject model (see table S2.6 and S2.8 in Supplementary Materials 2 for the 10 highest ranked models from the two model selections).

Global Best Model

The best global model based on the original explanatory variables included all the predictors and interaction effects between body mass and wind speed, between forearm length and precipitation, between T_a and ΔBP, between humidity and barometric pressure, between humidity and wind speed, between moon size and precipitation and between moon size and humidity (see Table 3 in Results for effect values). The interaction effects are visualized in Fig. S5.1.

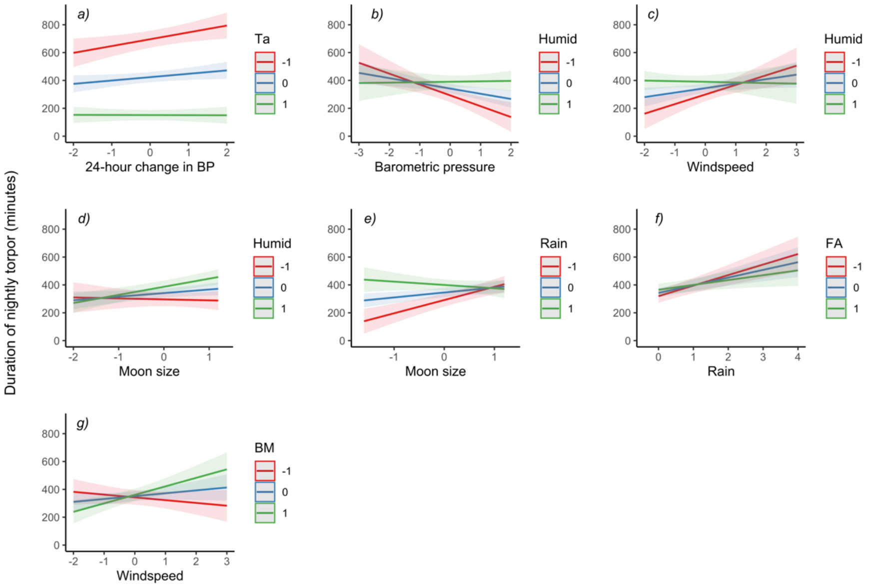

Figure S5.1: Interaction effects from the best global state model using the original explanatory variables including forearm length and body mass and their effects on weather condition impacts on the duration of nightly torpor, along with the interaction effects between environmental predictors. The colours correspond to the values 0 (blue), 1 (green), or -1 (red) for the scaled predictors explaining the effects.

Within-Subjects Model

The best within-subjects model using individually mean-centred explanatory variables included all the predictors and interaction effects between body mass and three of the environmental variables (wind speed, ΔBP, and precipitation) and between forearm length and precipitation (see Table 4 in Results for effect values). The interaction effects are visualized in Fig. S5.2.

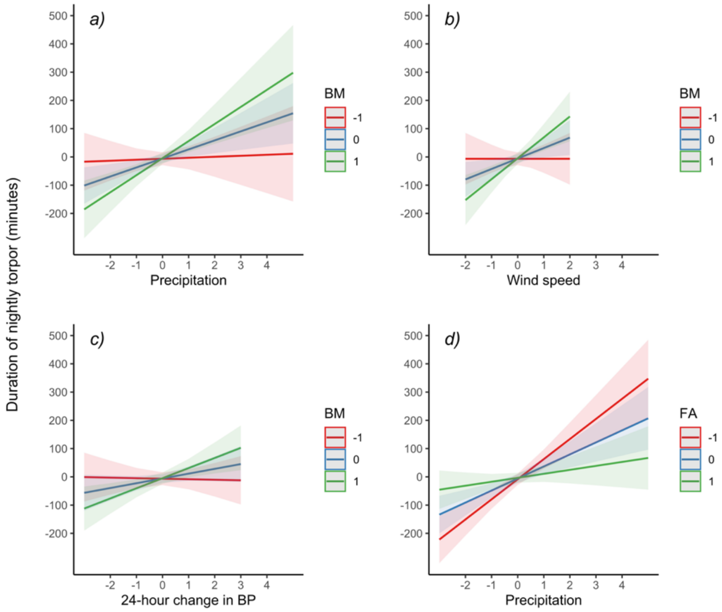

Figure S5.2a-d: Interaction effects from the best within-subject model including forearm length and body mass (in place of sex) and their effects on weather condition impacts on the duration of nightly torpor. The colours correspond to the values 0 (blue), 1 (green), or -1 (red) for the scaled predictors explaining the effects.

Weather Conditions from the Night Before and Temporal Autocorrelation

Moon disk illumination, barometric pressure and humidity showed strong temporal autocorrelations between their values at times t and t-1, which meant that only one of each version could be added at a time to the model. For humidity, the model including the values at t variable fitted the data better than the model including the values at t-1 variable (ΔAIC = 20.6). The models testing barometric pressure at time t and t-1 showed a slightly better fit for the model including the values at t variable, although the effects were similar in the two models (ΔAIC = 2.6). For the models including moon disk illumination at time t and time t-1, the model including moon light conditions from the previous night was a slightly better fit than the model with the values at t variable (ΔAIC = 1.8), but the effect sizes were almost identical.

In order to establish the degree of environmental temporal autocorrelation in our data, we calculated the Pearson correlation coefficient, using the *cor.test* function, between the different individually mean-centred weather variables and their values from 5 previous days. Additionally, we tested the correlation between individually mean-centred torpor use between time t and t-1. The correlation coefficients revealed that there were varying degrees of temporal autocorrelation present in the different environmental variables (Table S5.2). Moon disk illumination showed a strong temporal trend, which is to be expected as this variable is the equivalent to the changing moon phases. Barometric pressure showed high correlation between conditions at time t and time t-1 (correlation = 0.70) and some correlation between t and t-2 (correlation = 0.36), showing a cyclic pattern across the 5 previous days (Fig. S5.4). Humidity showed correlation between conditions at time t and time t-1 (correlation = 0.56) and also revealed a cyclic pattern across 5 consecutive days (Fig. S5.4). T_a, precipitation, wind and ΔBP all showed non-cyclic patterns and low levels of correlation in conditions comparing time t and up to 5 days earlier (correlation < 0.37). Torpor use on a given night was not strongly correlated with torpor use expressed on the previous night (correlation = 0.30, Fig. S5.5).

Table S5.1: Pearson correlation coefficient values between individually mean-centred conditions on a given night (t) and conditions from 5 previous nights (t-1 to t-5).

	Ta	Rain	Wind	Humidity	BP	ΔBP	Moon	Torpor
t-1	0.37	0.02	0.10	0.56	0.70	0.18	0.82	0.30
t-2	0.16	-0.23	0.02	0.15	0.36	-0.24	0.69	-
t-3	-0.08	-0.21	-0.04	-0.09	0.18	-0.21	0.58	-
t-4	0.03	-0.12	-0.17	-0.23	0.10	-0.10	0.47	-
t-5	0.05	-0.12	-0.04	-0.31	0.01	0.03	0.34	-

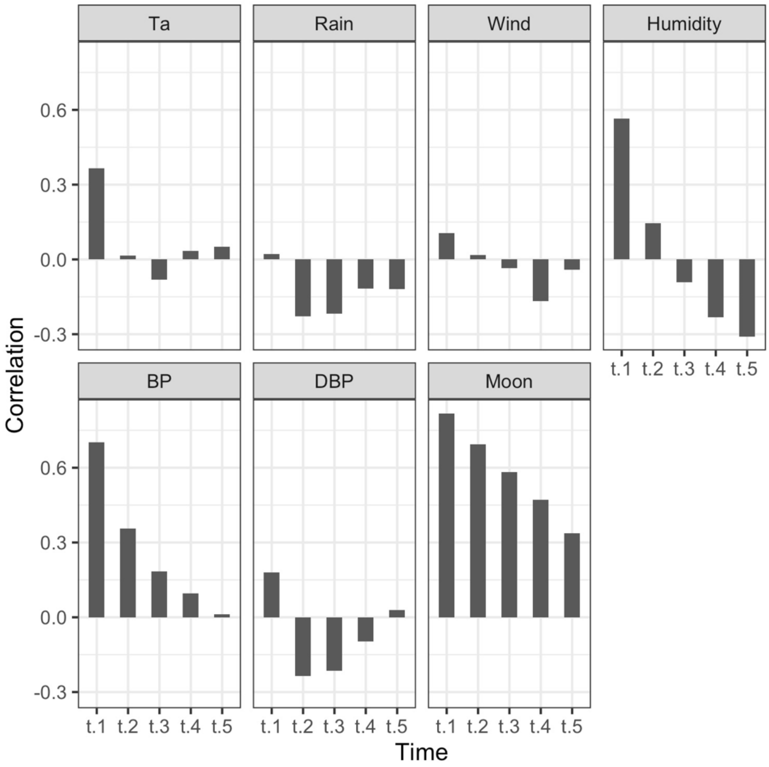

Figure S5.3: Correlation coefficients from Table S4.1, illustrating the temporal autocorrelation for each of the environmental variables for up to 5 days prior to the current conditions.

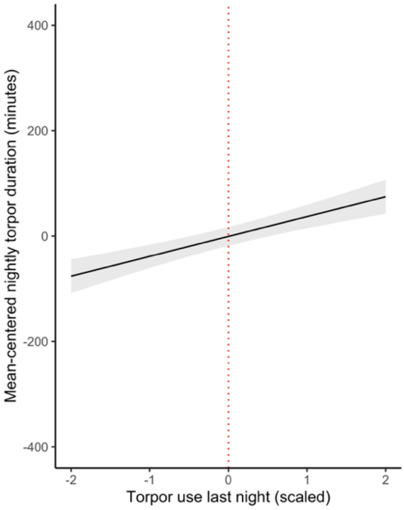

Figure S5.4: The effect of torpor use the night before (i.e. t-1, scaled) on the mean-centred torpor use on a current night when accounting for effects from the best within-subject model. The y-axis is fitted to the same range as Fig. 3 in Results to allow for direct comparisons with environmental effects at time t.

Paper II

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Determining the different phases of torpor from skin- or body temperature data in heterotherms

Mari Aas Fjelldal [a,*], Clare Stawski [a,b], Rune Sørås [a], Jonathan Wright [a]

[a] Department of Biology, Norwegian University of Science and Technology (NTNU), 7491, Trondheim, Norway
[b] School of Science, Technology and Engineering, University of the Sunshine Coast (USC), Maroochydore DC, Queensland, 4558, Australia

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ABSTRACT

Technological innovations have made heat-sensitive data-loggers smaller, more efficient and less expensive, which has led to a growing body of literature that measures the skin- or body temperatures of small animals in their natural environments. Studies of this type on heterothermic endotherms have prompted much debate regarding how to best define 'torpor' expressions from skin- or body temperature data alone. We propose a new quantitative method for defining torpor 'entries', 'arousals' and 'stable torpor periods' whilst comparing the results to 'torpor bout' durations identified using only the torpor cut-off method. By decomposing a torpor bout into 'entries', 'stable torpor periods', and 'active arousals', we avoid biases introduced by using strict threshold temperature values for the onset of torpor, thereby allowing better insight into individual use of torpor. We present our method as an easy-to-use function written in R-code, offering an un-biased and consistent methodology to be applied on skin- or body temperature measurements across datasets and research groups. When testing the function on a large dataset of skin temperature data collected on three bat species in Norway (*Plecotus auritus*: $N_{ind} = 39$; *Eptesicus nilssonii*: $N_{ind} = 11$; *Myotis brandtii*: $N_{ind} = 10$), we identified 461 complete torpor bouts across species. More than 40% of the torpor bouts ($N_{bouts} = 192$) did not contain stable torpor periods, because the bats aroused before they had reached a stable skin temperature level. Furthermore, only considering 'torpid' and 'euthermic' temperature values by applying strict cut-off thresholds led to potentially large underestimations of torpor bout durations compared to our quantitative determination of the onset and termination of each torpor bout. We highlight the importance of differentiating between torpor phases, especially for active arousals that can be very energetically expensive and may alter our evaluation of the actual energetic savings gained by an individual employing torpor.

1. Introduction

For small endotherms with high mass-specific energetic demands, decreasing energetic expenditure through temporal heterothermic responses have proven to be one of the most efficient energy-saving strategies available across species (Heldmaier et al., 2004). By employing daily torpor and long-term hibernation, heterothermic endotherms may reduce their energy consumption to a small fraction of their euthermic levels, depending upon ambient temperatures (T_a) (Geiser, 2004; Heldmaier et al., 2004). These large energy savings are made possible through temporal and reversible reductions in correlated physiological processes like respiration, heart rate and thermogenesis (Lyman et al., 1982). However, due to various ecological and physiological costs associated with torpor and hibernation (Humphries et al., 2003; Boyles et al., 2020; Landes et al., 2020), there are likely to be trade-offs that lead to adaptive variation in the strategic use of heterothermic responses across species and individuals.

'Torpor' as a physiological state can be quantified with high accuracy using various monitoring methods in the laboratory; however, individuals in captivity have been found to express shorter and shallower daily torpor than free-ranging individuals, potentially due to higher gut-fill levels and persistent awareness when in captivity (Geiser et al., 2000). The measurement and quantification of torpor use in heterothermic endotherms in the wild is therefore crucial for understanding the strategic employment of this energetic strategy as a response to natural intrinsic and extrinsic factors. However, measuring heterothermic responses in free-ranging animals is more limited in terms of available methods, particularly in small-bodied species, which comprise

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* Corresponding author.
E-mail address: mari.a.fjelldal@ntnu.no (M.A. Fjelldal).

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the majority of heterotherms that express daily torpor (Geiser and Ruf, 1995). Monitoring heart rates and metabolic rates usually demands advanced technical equipment more suited to laboratory conditions, although rapid technological innovations may also make such methods more available for field studies in the future (see Butler et al., 2004; Reher and Dausmann, 2021).

A simpler current method frequently used to assess instances of torpor in field studies on small-bodied animals is the measurement of body temperature (T_b) through surgical tag implantations (McCafferty et al., 2015) or skin temperatures (T_{skin}) using external temperature-sensitive transmitters (Barclay et al., 1996; McCafferty et al., 2015). Because torpid animals do not defend a high T_b, periods of measured T_{skin} or T_b below expected euthermic levels can be used as indicators of the animal expressing torpor, although the determination of torpor from body temperature data alone has its challenges (Barclay et al., 2001; Canale et al., 2012). Further, the existence of a variety of metrics executed in various ways across studies and research groups has made comparisons of heterothermic responses between species challenging (see Boyles, 2019).

One of the most frequently applied methods for identifying torpor bouts from T_{skin} or T_b data is to use threshold values, assigning all values below a certain critical temperature as indicative of torpor and anything above it as euthermic. Unfortunately, the lack of a common definition in this case has led to a diversity of different body temperature thresholds being used, from the use of “active” temperatures (the T_b recorded immediately prior to departure from roost; Barclay et al., 2001) to torpor onset values calculated using lab-derived equations (Willis, 2007), and in many cases various seemingly “arbitrary” cut-off values appear to have been applied (reviewed by Barclay et al., 2001). Nevertheless, it remains one of the easiest metrics to apply, and although this may not be an optimal metric for direct comparisons of torpor use between species (see Boyles, 2019) it still provides good estimates within populations or species if the cut-off values are chosen sensibly (Brigham et al., 2011).

An overlooked aspect with this method, however, is that torpor bouts themselves consist of different phases as individuals (i) gradually ‘enter’ torpor with declining body temperatures, (ii) remain for a period at ‘stable’ torpid body temperature, and (iii) ‘arouse’ out of torpor with increasing body temperatures, each of which will differ greatly in their energetic characteristics (see Utz et al., 2007; Geiser et al., 2014; Menzies et al., 2016). Specifically, animals that arouse by producing body heat and actively rewarm more quickly from deep torpor can experience large energetic and physiological costs that differ greatly from energy expenditure at stable torpor levels (Currie et al., 2015). Furthermore, torpor entries and active arousals usually take the form of sigmoidal body temperature curves (Utz et al., 2007; Nicol and Andersen, 2008). In many cases, this means that the start of any torpor entry and the end of any rewarming will be occurring at body temperatures well above the particular torpor cut-off value, resulting in parts of these phases of torpor expression being excluded from the torpor bout. This can be problematic, especially for short torpor bouts that are frequently expressed by many daily heterotherms and by hibernators outside of the hibernation season. Large proportions of a torpor bout may thus be completely overlooked without further evaluation of the data when applying strict cut-off values.

A metric that allows for the identification of cooling and warming periods from T_b or T_{skin} measurements in heterotherms is the nonstationary waveform analysis (Refinetti, 2004; Levesque et al., 2017). Through analysing wave-form patterns from T_b or T_{skin}, this method offers descriptions of temporal thermoregulatory patterns that are comparable across species. However, the complexity of such metrics may prevent many researchers from applying them to their datasets. It is also unclear how well such methods work on datasets containing various lengths of missing data (D. Levesque, personal communication, September 15^{th} 2022), which is something that most field datasets will inevitably contain.

Here, we present a simplified method for identifying the different phases of a torpor bout from T_{skin} or T_b data alone, dividing it into torpor ‘entries’, ‘stable torpor’ periods and active torpor ‘arousals’. By considering the immediate temperature changes between datapoints we developed a temperature differential method that, based on the rate of change between points and on the temperature in relation to a specified torpor threshold value, can determine the different stages of a torpor bout. Temperature differential methods have previously been presented to describe thermoregulatory patterns (Utz et al., 2007; Gordon, 2009), but they are either not necessarily suitable for describing torpor expressions or may be difficult to properly apply to field-derived data, where the thermal micro-environment around the torpid animal often is impossible to monitor. Our quantitative determination of torpor phases and various phase-types was developed using an extensive dataset of T_{skin} collected in the field on three bat species across three summer seasons in Norway. With this method, included as an easy-to-use function in R-code (R Core Team 2018), we hope to improve the way data analyses are carried out on torpor data collected as part of field energetics studies, such that important aspects of torpor bouts can be further understood beyond what is currently possible by simply considering T_b or T_{skin} to be above or below a certain threshold.

2. Methods and results

Permits to undertake the fieldwork were given by the Norwegian Food Safety Authority (FOTS ID 23284) and the Norwegian Environment Agency (ref. 2018/4899).

2.1. Data collection

We collected T_{skin} data from three bat species during summer in 2019–2021 at multiple locations in Norway: 39 brown long-eared bats (*Plecotus auritus*; 12 males and 27 females) were studied during June and July across all three years in Nittedal, Norway (60.05° N, 10.87° E). Eleven northern bats (*Eptesicus nilssonii*) were captured at two study sites: data from two individuals (one male and one female) were collected in Nittedal (June 2019 and June 2021), while data from nine individuals (seven males and two females) were collected in Trondheim, Norway (63.43° N, 10.40° E) during June, July, and August in 2020 and 2021. Ten Brandt’s bats (*Myotis brandtii*) were studied at two study sites: data from four females were collected in Nittedal during July 2020, while data from six females were collected during August at a location south of Trondheim (63.17° N, 9.48° E).

All bats were captured using mist-nets put up before sunset along tree corridors or within forest openings. The nets were monitored continuously using bat detectors and frequent visual checks to avoid captured bats hanging unattended for prolonged periods of time. Captured bats were subsequently fitted with temperature-sensitive radio-transmitters (~0.5g, PIP31, Lotek Wireless Inc., Dorset, U.K.) by trimming fur from their dorsal region and attaching the tags using a skin adhesive (B-530 Adhere Adhesive or Sauer-Hautkleber 50.01, Manfred Sauer GmbH, Lobbach, Germany). Each transmitter had been calibrated in water baths (0 °C–45 °C with stepwise increases of 5 °C) prior to capture nights. After tagging, the bats were released at the capture site. Each morning the bats were tracked using radio-telemetry to find their current day roosts, where we placed remote data-loggers that recorded the pulse-intervals from the transmitters every 10 min. Based upon the calibration, we then converted the recorded pulse-intervals into T_{skin} measurements. Transmitters were kept on the animals between 1.5 and 19 full days (median duration: 6.5 days). T_a outside the roost was also recorded using small temperature-loggers (0.5 °C, DS, 1921G Thermochron iButtons, Maxim Integrated Products, Inc., Sunnyvale, CA, USA) hung inside cardboard cups from tree branches ~1.5–2 m above ground to avoid direct sunlight.

2.2. Defining torpor-entries and -arousals

We first applied equation (1) developed by Willis (2007) for identifying torpor onset (T_{onset}) temperature values from our measured T_{skin} data:

$$T_{onset} - 1SE = (0.041) \times BM + (0.040) \times T_a + 31.083. \qquad (1)$$

We calculated T_{onset} values for each bat day, thus taking into account individual body mass (one measurement per bat) and daily mean T_a (measured outside of the roosts), resulting in daily T_{onset} values ranging from 31.8 °C to 32.4 °C across all individuals and days for brown long-eared bats, 31.7 °C–32.6 °C for northern bats, and 31.8 °C–32.2 °C for Brandt's bats. More accurate daily T_{onset} values would, however, require daily measurements of body mass and preferably a stable daily T_a measured in the roost. As we had neither, we chose to calculate species-specific T_{onset} values by calculating the mean of the daily T_{onset} values, which was further supported by the relatively small variation seen in the T_{onset} values calculated for each species (i.e. T_{onset} ranges reported above). Because equation (1) is based upon true T_b recordings with internal sensors, and as $T_b - T_{skin}$ measurements are often < 2 °C for small mammals (Audet and Thomas, 1996; Barclay et al., 1996), we subtracted 2° and calculated species-specific T_{onset} values of 30.1 °C for brown long-eared bats, 30.1 °C for northern bats and 29.9 °C for Brandt's bats.

Second, to avoid the problem of strict cut-offs where all T_{skin} above T_{onset} were defined as euthermic and all T_{skin} below as torpor, we looked at the different phase characteristics from each identified torpor bout. The decrease in T_{skin} normally started well above the T_{onset} value as the bats entered a torpor bout, and increased well above the T_{onset} value when they were arousing from the bout (see Fig. 1a). Based upon quantitative criteria, we therefore divided torpor bouts into three phases: entries, torpor, and arousals. An 'entry' into a torpor bout was defined as all T_{skin} values where the change from the previous measurement (ΔT_{skin}) was $\geq -0.6\ °C\ \text{min}^{-10}$, starting out from the first T_{skin} datapoint that had a value below the T_{onset} value and finding the start of the entry by going backwards in time from this point until $\Delta T_{skin} < -0.6\ °C\ \text{min}^{-10}$, while the end of the entry was located by similarly going forward in time. 'Arousals' from torpor were defined similarly and included all values with a $\Delta T_{skin} \geq 0.6\ °C\ \text{min}^{-10}$, going backwards from the last T_{skin} datapoint that had a value below the T_{onset} value to find the start of the arousal and forward to find the end. However, as entries and arousals sometimes momentarily slowed up for one measurement (i.e. for one 10min period in our dataset) before speeding up again, the ΔT_{skin} threshold ($-0.6\ °C\ \text{min}^{-10}$ for entries and $0.6\ °C\ \text{min}^{-10}$ for arousals) needed to be passed by two consecutive readings to record it as the clear start or end of an entry or arousal phase. Fig. 1 illustrates an example where the different phases of a torpor bout are shown as the recorded T_{skin} values (Fig. 1a) and as the corresponding ΔT_{skin} values (Fig. 1b).

The choice of starting or ending each phase based upon a ΔT_{skin} value of $>0.6\ °C\ \text{min}^{-10}$ is justified through the following arguments. Utz et al. (2007) reported that the onset of an arousal (or "instantaneous rate of rewarming") commonly started with a ΔT_{skin} of $0.02\ °C\ \text{min}^{-1}$. Applying this rate to our 10-min interval data would lead to the definition of an arousal normally starting around a ΔT_{skin} of $0.2\ °C\ \text{min}^{-10}$. However, as the exact thermal environment of free-ranging individuals is uncontrolled and, in our case, unmonitored, there is a risk of including many cases of passive rewarming when identifying 'active arousals' if the ΔT_{skin} definition value of when active arousal begins is too low (see for example, Figure S1.1 in the Supplementary Materials 1). Passive rewarming more closely resembles stable torpor periods than active arousals when it comes to energetic expenditure (Currie et al., 2015), which means that it is often better to include these types of passive arousals as part of the stable torpor period rather than as part of any active rewarming. We thus term all identified rewarming torpor phases in this article as 'active arousals' rather than simply 'exits' from torpor, due to the ΔT_{skin} threshold preventing rewarming with lower rates to be included. However, without monitoring the temporal fluctuations in the thermal environment directly surrounding the torpid animal, we cannot guarantee that our method does not include small periods of passive rewarming, especially if the thermal environment around the torpid animal is heating up at an unusually high rate.

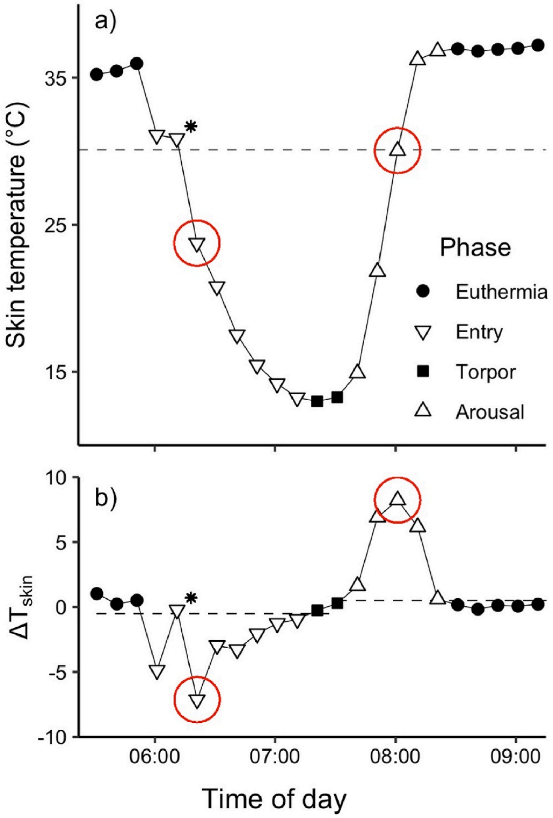

Fig. 1. Example of a torpor bout from the brown long-eared bat data, with the different phases indicated. **a)** Exact T_{skin} measurements during the torpor bout. The dashed horizontal line indicates the calculated T_{onset} value of 30.1 °C. **b)** ΔT_{skin} values (difference in °C from previous datapoint) during the same torpor bout. The dashed horizontal line during the torpor entry indicates the threshold of $-0.6\ °C\ \text{min}^{-10}$ for entry points, while the dashed horizontal line during the torpor arousal indicates the threshold of $0.6\ °C\ \text{min}^{-10}$ for arousal points. Red circles mark the first (for the entry) and last (for the arousal) recorded T_{skin} measurement being below the T_{onset} value. Going backward and forward in time from these datapoints, all datapoints with a $\Delta T_{skin} \leq -0.6\ °C\ \text{min}^{-10}$ or $\geq 0.6\ °C\ \text{min}^{-10}$ were considered part of the torpor entry or arousal, respectively. However, datapoints needed to be $> -0.6\ °C\ \text{min}^{-10}$ or $< 0.6\ °C\ \text{min}^{-10}$ for two consecutive readings for the end or start of the phase to be recorded. In the torpor entry the datapoint marked with * had a $\Delta T_{skin} < -0.6\ \text{min}^{-10}$, but as this was not true for two consecutive points it was included as part of the entry.

The final definition of a ΔT_{skin} threshold value $> 0.6\ °C\ \text{min}^{-10}$ for the start/end of each phase was decided upon after testing the method using ΔT_{skin} threshold values ranging between $0.1\ °C\ \text{min}^{-10}$ to $1.2\ °C\ \text{min}^{-10}$ and visually exploring at which point the phase durations first stabilized (see Fig. S1.2 in the Supplementary Materials 1). When applying our suggested metric to other datasets we strongly encourage that the sensitivity analyses are performed over again (codes are included in the r-script in the Supplementary Materials), adjusting the values to better fit the data.

There were clear additional differences among the types of torpor entry- and arousal-phases we recorded, and so we divided them into four categories (see Fig. 2 for examples):

1. 'Complete' for phases with no missing datapoints, exclusively negative ΔT_{skin} values for entries and positive ΔT_{skin} values for active arousals, and with the start of entries or the end of arousals being above the T_{onset}.
2. 'Mixed' for phases with no missing datapoints, start or end of phase above T_{onset}, but which had single datapoints with a shift in direction of ΔT_{skin} (single positive values for entries and single negative values for arousals). However, datapoints with a shift in direction would only be included as part of the phase if the following T_{skin} value was lower than the T_{skin} value before the shift (for entries) or higher than the T_{skin} value before the shift (for arousals).
3. 'Within bout' for phases with no missing datapoints, with a maximum negative $\Delta T_{skin} \leq -1.5\ ^{\circ}C\ min^{-10}$ (for entries) or maximum positive $\Delta T_{skin} \geq 1.5\ ^{\circ}C\ min^{-10}$ (for arousals), but which did not start (for entries) or end (for arousals) above the T_{onset}. After identifying any such datapoints within torpor bouts, further values in either direction were included to the phase if the ΔT_{skin} were within the general ΔT_{skin} threshold of 0.6 min^{-10}. The requirement of a maximum positive or negative ΔT_{skin} of 1.5 °C min^{-10} was implemented to reduce the risk of 'passive' phases being included (see further explanation in section 1.3 in the Supplementary Materials 1). The exact 'within bout' threshold value was decided upon in the same manner as described for the ΔT_{skin} threshold value of 0.6 min^{-10} above (see Fig. S1.3 for sensitivity testing).
4. 'Not complete' for phases that were missing datapoints.

Complete torpor bouts were further identified based on the presence of an entry and a following arousal, including any stable torpor periods and middle-of-bout phases between the torpor entry and arousal as part of the torpor bout. We detected one or two special cases in our dataset where the identification of complete torpor bouts was overlooked, see Supplementary Materials 2 for examples. However, in most cases the identification of complete torpor bouts was accurate. For stable torpor periods we allowed up to four missing datapoints to be considered as part of the torpor bout, but only if the last recorded T_{skin} and the next recorded T_{skin} both were below the T_{onset}. The number of missing datapoints that should be allowed as part of a torpor bout may depend on the interval of which the measurements have been recorded, and is likely to be a question of preference for each individual researcher and/or dataset. In our constructed function written in R-codes we have therefore included an option for specifying the number of missing values that will be allowed when determining stable torpor periods. We encourage transparency and that anyone employing our codes to their dataset states the number of missing values that they allowed, in addition to their choice of ΔT_{skin} thresholds.

2.3. Distribution and characteristics of torpor phases

Only complete torpor bouts were considered here, thus excluding torpor periods with no recorded entry or arousal, or which contained a number of consecutive missing values that exceeded the specified tolerance. This resulted in a total sample size of 461 torpor bouts across 52 bats (*P. auritus*: $N_{bouts} = 378$, $N_{ind} = 36$; *E. nilssonii*: $N_{bouts} = 54$, $N_{ind} = 8$; *M. brandtii*: $N_{bouts} = 29$, $N_{ind} = 8$). Because 'within bout' arousals and re-entries were included in the data for the different phases of torpor the numbers of entry and arousal phases were larger than the number of torpor bouts they were taken from ($N_{entries} = 592$, $N_{arousals} = 573$).

As the total duration of complete torpor bouts (which included all

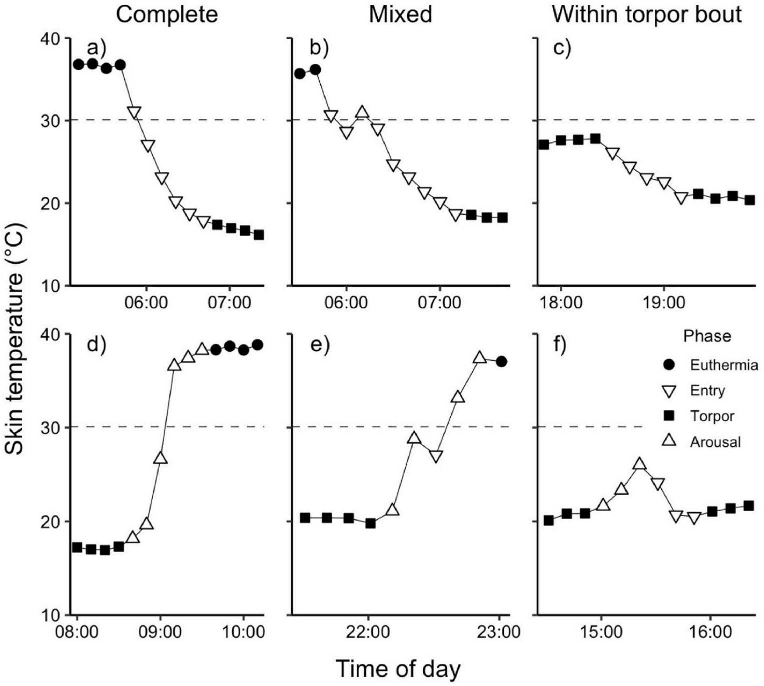

Fig. 2. Examples from data on brown long-eared bats of torpor entries and arousals from the different categories. **a)** A complete torpor entry, **b)** a mixed torpor entry, **c)** a within-bout torpor entry (values < T_{onset}), **d)** a complete torpor arousal, **e)** a mixed torpor arousal, and **f)** an example of arousal and torpor entry within a torpor bout (values < T_{onset}). The horizontal dashed line indicates the T_{onset} value of 30.1 °C for brown long-eared bats. The fourth category 'Not complete' is not shown.

phases, also ‘within bout’ phases) varied largely, from 20 min to 57.5 h (median duration: *P. auritus* = 70 min; *E. nilssonii* = 130 min; *M. brandtii* = 80 min), so did the proportion of each phase within each torpor bout (Fig. 3a). With increasing duration of torpor bouts, the proportion of time bats spent in stable torpor consequently also increased, while the relative proportion of time spent entering or actively arousing from torpor decreased accordingly (Fig. 3b). Although this is a logical and expected outcome, with longer torpor bouts consisting of longer periods of stable torpor, it highlights the issue of short torpor bouts necessarily consisting largely of entry and arousal durations.

As many as 192 of all the torpor bouts lacked stable torpor periods altogether (the zero percentages in the middle panel of Fig. 3b), although this was only observed in torpor bouts that had a total duration of ≤2 h and 10 min. In these torpor bouts, bats started to cool down after initiating torpor, but rewarmed again before they reached a stable T_{skin} level. The fastest rates of cooling (for torpor entries) across species ranged from −0.6 °C min^{-10} to −10.8 °C min^{-10} (mean fastest rate: −4.0 °C min^{-10} ± 2.1), while the fastest rates of rewarming (for torpor arousals) ranged from 0.6 °C min^{-10} to 17.2 °C min^{-10} (mean fastest rate: 4.3 °C min^{-10} ± 2.4), as shown in Fig. 3c.

To further explore phase characteristics we sampled all recorded phases in the dataset, including phases that did not belong to complete torpor bouts, although phases categorized as ‘Not complete’ were excluded. This led to a total sample size of 731 torpor entries and 671 active arousals. The most frequently expressed type of torpor entry and active arousal across species was the ‘Complete’ phase type, although ‘Within bout’ phases were recorded at high frequencies (Table 1). The recorded duration of the different phases here varied from 10 min to 170 min for torpor entries (mean duration across categories and species: 33.7 min ± 28.7), and from 10 min to 200 min for active arousals (mean duration across categories and species: 30.8 min ± 28.2).

2.4. *Comparing methods for estimating torpor bout durations*

Because our method provides an extension to an already existing metric (the torpor cut-off method) we wanted to investigate the impact that the two different methods would have on the evaluation of torpor expressions in our dataset. We therefore compared estimated durations of torpor bouts using two different definitions:

1. A torpor bout would last from the onset of the torpor entry until the end of the torpor arousal;
2. A torpor bout would last from the first T_{skin} measurement below the T_{onset} value until the last T_{skin} measurement below the T_{onset} value.

The two definitions yielded large differences in the estimated duration of the same torpor bouts (Fig. 4). The torpor bouts were estimated to last between 10 and 140 min longer (mean ΔTorpor bout duration: 35.5 min ± 24.3) when including all three phases as part of a torpor bout (definition 1) compared to applying strict cut-off values (definition 2; Fig. 4).

We further attempted to compare the phase determinations provided by our method to the ones identified by the non-stationary waveform analysis, as described in Levesque et al. (2017). Unfortunately, we were unable to retrieve sensible results for datasets such as ours when applying this method, possibly due to the inaccurate calculation of quantiles caused by frequent periods of missing data (in data like ours the signal disappears whenever the bats leave their roosts to forage at night). We were therefore unable to directly compare the two metrics on our data.

3. Discussion

We here describe a simplified method for separating torpor bouts into different phases (torpor ‘entries’, ‘stable periods’, and ‘active arousals’) based upon T_{skin} or T_b data alone, and provide a function written in R-codes to allow others to easily apply our proposed method to their datasets (see R-script in Supplementary Materials). We tested the method on a large dataset containing T_{skin} data collected from three different free-ranging Norwegian bat species, which resulted in the identification and dissection of 461 complete torpor bouts across species. Our method for dividing torpor bouts into phases will hopefully improve existing torpor cut-off methods for identifying torpor bouts, and especially the contrastingly different phases within these bouts, in order to improve the evaluation of torpor expression and energetics from field-derived data on T_{skin} or T_b data in heterothermic endotherms.

In our dataset we further showed that recordings of torpor bouts could be placed into different data categories (‘Complete’, ‘Mixed’, and ‘Within torpor bout’). The differentiation of torpor entries and arousals into the categories ‘Complete’ and ‘Mixed’ are perhaps less important for assessing torpor energetics, but they are presented here to show important distinctions within torpor T_{skin} or T_b data when identifying each phase of a torpor bout. However, torpor entries and/or arousals being expressed within torpor bouts should perhaps always be distinguished from these same phases, given that they do not mark the

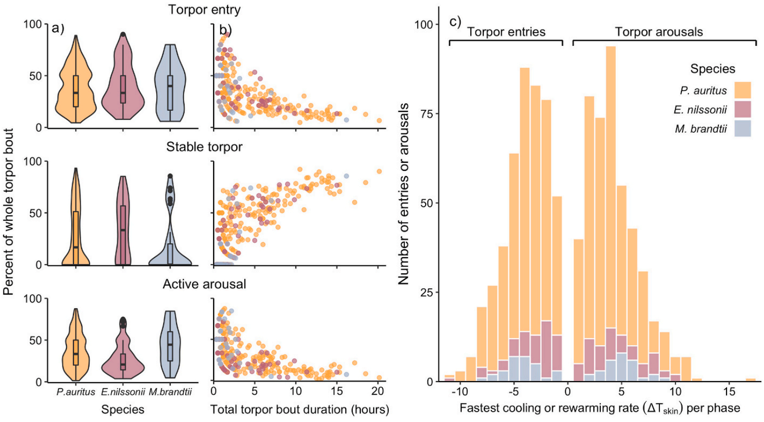

Fig. 3. Distribution and characteristics of torpor ‘entries’, ‘stable torpor’ periods and ‘active arousals’ across the three bat species. **a)** Violin plots showing the distribution of each phase against the percentage they make up of the whole torpor bout duration for each of the species. Medians, 25th and 27th percentiles and minimum and maximum values are shown within the violin plots. **b)** The percentage of how much each phase makes up of the whole torpor bout as a function of total torpor bout duration. Increasing torpor bout durations consists of increasing periods of stable torpor, while shorter torpor bouts consist largely of entries and active arousals. *Note*: the two longest torpor bouts in the dataset are excluded from Fig. 3b for visualization purposes, as these were 57.5 and 49 h, with the stable torpor period covering respectively 85.2% and 93.2% of the total torpor bout duration. **c)** Distribution-plot of the fastest cooling (maximum negative ΔT_{skin} for entries) and rewarming rates (maximum positive ΔT_{skin} for arousals) for each torpor entry and arousal across species. These rates indicate differences in T_{skin} between datapoints measured with 10 min intervals.

Table 1
Overview of the proportion of each of the three data categories for torpor entries and active arousals, and duration characteristics across the three bat species. Note that the phases belonging to the 'Mixed' category only started from 30 min due to the way this category is defined (phases need one datapoint with a shift in direction).

	Torpor entries			Active arousals		
	Complete	Mixed	Within bout	Complete	Mixed	Within bout
P. auritus						
Number of phases	316	93	195	315	60	175
Mean duration (minutes)	27.4 ± 24.5	59.5 ± 29.6	26.7 ± 21.6	28.8 ± 25.3	60.5 ± 29.1	21.8 ± 16.9
Median duration (minutes)	20	50	20	20	50	20
Range duration (minutes)	10–130	30–150	10–130	10–150	30–180	10–120
E. nilssonii						
Number of phases	53	11	17	54	8	15
Mean duration (minutes)	44.2 ± 36.9	78.2 ± 35.7	38.8 ± 37.7	37.0 ± 40.7	87.5 ± 60.4	24.0 ± 20.3
Median duration (minutes)	30	80	30	20	65	10
Range duration (minutes)	10–160	30–150	10–170	10–200	30–200	10–70
M. brandtii						
Number of phases	25	5	16	27	3	14
Mean duration (minutes)	29.2 ± 20.8	46.0 ± 13.4	25.0 ± 25.3	26.3 ± 18.8	46.7 ± 5.8	20.0 ± 18.8
Median duration (minutes)	30	40	10	20	50	10
Range duration (minutes)	10–90	30–60	10–100	10–70	40–50	10–80

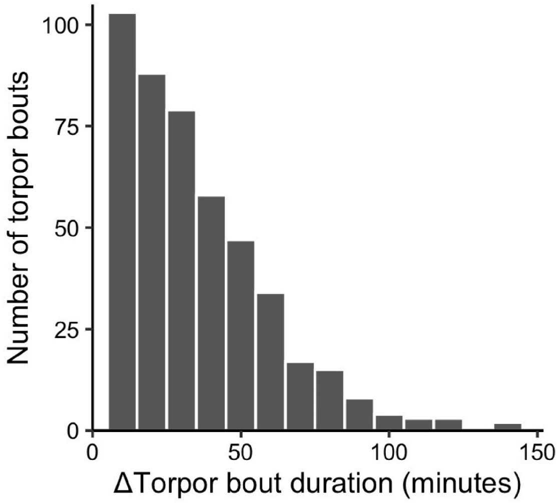

Fig. 4. The difference for torpor bout durations (minutes) estimated with definition 1 (by assessing entries and arousals) minus the duration estimated with definition 2 (using a single threshold ΔT_{skin} value).

beginning or the end of a torpor bout. Such within-bout arousal/entry events are not frequently reported in the literature, although partial arousals have previously been described in several heterothermic species (e.g. Twente and Twente, 1965; Snapp and Heller, 1981; Nestler, 1990; Geiser and Brigham, 2000). However, it is not always clear what would cause torpid animals to occasionally change their torpor depth or temporarily arouse and re-enter to their previous temperature depth without going through a full rewarming to euthermic temperature levels. Assuming that these events are in fact the results of individuals actively altering their metabolic thermogenesis (see definition of category 3 for justification), such within-bout entries and arousals might be the result of temporary disturbances or of the need to strategically adjust torpor depth based upon the individual's current physiological state, environmental conditions or future foraging prospects. However, without proper monitoring of the torpid individuals and their immediate surroundings, it is impossible to draw any firm conclusions along these lines from T_{skin} or T_b data alone.

Studies using skin or body temperature data to quantify torpor use in free-ranging heterotherms have so far mainly highlighted the challenges in determining whether an animal is torpid or euthermic (Barclay et al., 2001; Willis and Brigham, 2003; Boyles et al., 2011; Canale et al., 2012), and so they have largely ignored the differentiation of torpor bouts into the different stages of entry, stable periods and arousals (but see Levesque et al., 2017). This is problematic for two main reasons. Firstly, applying a strict cut-off threshold may exclude parts of a torpor bout as they often start or end high above the T_{onset} temperature (see Figs. 1a and 2), which for short torpor bouts can lead to the duration of a torpor bout (and its energetic consequences) to be largely underestimated. Daily torpor expression in bats outside of the hibernation season often consist of frequent but short periods of torpor (see Stawski and Geiser, 2010; Johnson and Lacki, 2014; this study), which means that the risk of underestimating the overall torpor expression is likely to be an issue in large parts of the literature. Secondly, to assume that all assigned torpor measurements below an applied threshold share energetic characteristics, even after accounting for the effects of ambient temperature, would in most cases prove incorrect. This is particularly true of the potentially high costs of active arousal (i.e. in relation to stable period torpor energetics) as the individual rewarms from torpor (Geiser et al., 2014; Currie et al., 2015). The simultaneous steep increases in heart rate, oxygen consumption and T_b during arousals indicate that T_{skin} or T_b provide useful indicators of increased energy consumption, as long as any periods of passive rewarming are excluded (Currie et al., 2014, 2015).

Cooling during torpor entry is, in contrast, perhaps not all that distinguishable in terms of energetic costs from stable torpor periods. This is because other physiological traits, like heart rate and oxygen consumption, seem to fall to low levels before the T_b has had the time to decrease substantially, suggesting that by the time a larger drop in temperature is recorded the metabolic rate has already been drastically lowered (see Nestler, 1990; Bartels et al., 1998; Currie et al., 2014; Geiser et al., 2014; Currie et al., 2015). The distinctive energetics involved in active arousals compared to stable torpor periods, and the not so distinctive energetics of torpor entries, mean that when studying torpor bouts using T_{skin} or T_b measurements alone, the different phases of the torpor bout need to be defined using more detailed methods like the one we propose.

The criteria used for determining which datapoints should and should not be included as part of a torpor bout is important to consider in light of various specified and unspecified assumptions (see above). When applying two different definitions of a torpor bout (1. all phases included; 2. strict cut-off at T_{onset}) to the 461 torpor bouts identified in our dataset, we showed that potentially large differences in the estimations of torpor durations, and consequently timing of events, were possible. Only applying a cut-off T_{onset} value without considering the temporal characteristics between datapoints led to potentially large under-estimations of torpor bouts when comparing it to our new suggested method of identifying all phases. It is not necessarily better to include all the phases in any analyses of torpor bout durations, given the potentially large energetic differentiation of active arousals, but we argue that each phase should be clearly identified so that the decisions on which datapoints to include in various statistical approaches are made intentionally with regard to what is being investigated. Future studies that consider using strict cut-off values for identifying torpor bouts should, therefore, extend their methods by applying our proposed metrics in order to clearly evaluate the different characteristics of torpor bout expressions.

Our method should, however, be considered in light of its potential applicability before deciding on which metrics to use on a given dataset. Because it is an extension of the torpor cut-off method, our metric faces the same limitations to multispecies comparisons as the cut-off method (see Boyles, 2019). For general cross-species comparisons of thermoregulatory cycles in heterotherms it may therefore be more appropriate to perform nonstationary waveform analyses as described in Levesque et al. (2017), if possible. However, for studies that need to apply cut-off values to their data in order to describe torpor bouts, we believe that our method will improve descriptions and comparisons of torpor expressions within individuals and populations. Datasets with larger sampling intervals (e.g. results presented in this study are based upon 10-min intervals) still need to be treated with caution when applying our proposed method. This is because larger intervals can result in larger uncertainty in the determination of the exact timing of any torpor bout, which will lead to the differentiation of each phase being less accurate. Further, it might still be necessary to validate and test the method by conducting lab-experiments, where T_b or T_{skin} data is recorded with various logging frequencies across various temperature cycles, in order to fully understand the exact limitations of this metric.

Although the proposed method in this study does not solve all of the current issues with the initial detection of torpor bouts from T_{skin} or T_b data alone (see Barclay et al., 2001; Boyles et al., 2011), identifying ‘entry’, ‘stable’ and ‘arousal’ torpor bout phases does improve upon the use of strict threshold values that can result in inaccurate measures of the durations and energetic consequences of torpor bouts. With our suggested method, the implementation of T_{onset} values is only used in the initial identification of torpor events, and before determining the ‘true’ start and termination of these bouts, which would be independent of any original T_{onset} value. This method could therefore perhaps help future studies arrive at a more comparable definition of torpor expression in T_{skin} or T_b data from free-ranging individuals. Accurately determining the timing of when daily heterotherms enter and actively arouse from torpor is also important because it should reflect strategic evaluations of the cost-benefit ratio they perceive given current and prospective state, environmental conditions and foraging opportunities. Although a phase-differentiation might be of less importance in long-term hibernation events, we hope that this proposed method will further improve our understanding and evaluation of energetic decisions made by heterotherms in their natural environment.

Data accessibility statement

The datasets used to test our proposed method in the current study are available from the corresponding author on reasonable request. The R-codes for applying the method on other datasets are made available in the Supplementary Materials.

Author contributions

Mari Aas Fjelldal: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing - original draft. **Clare Stawski**: Conceptualization, Validation, Funding acquisition, Supervision, Writing- Reviewing and Editing. **Rune Sørås**: Data curation, Writing- Reviewing and Editing. **Jonathan Wright**: Conceptualization, Investigation, Supervision, Writing- Reviewing and Editing.

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Ethical approval

All applicable institutional and national guidelines for the care and use of animals were followed (see “Methods & Results” for permit information).

Declarations of competing interest

We declare no conflict of interest.

Data availability

The data used to test our method are available from the corresponding author on reasonable request. The R-codes for applying the method on other datasets are available in the Supplementary Materials.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2022.103396.

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Supplementary Materials 1: ΔT_{skin} threshold sensitivities

1.1 Example of a passive rewarming

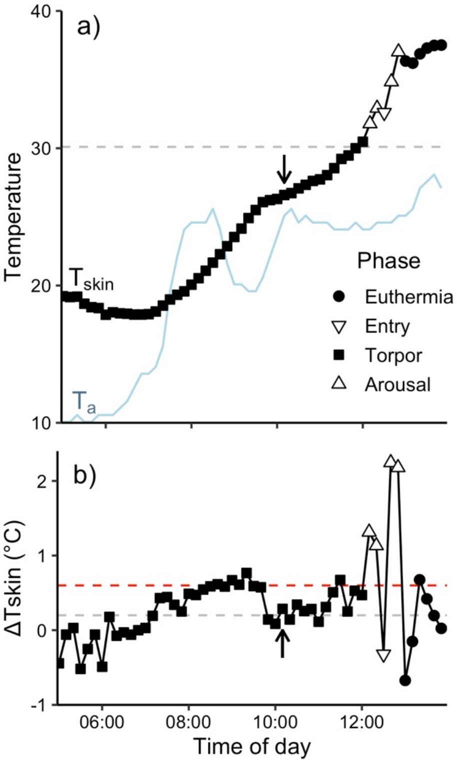


Figure S1.1: Example of a torpor bout in a brown long-eared bat where the increased T_{skin} prior to the active arousal is likely a result of passive rewarming via increasing T_a. **(a)** T_{skin} (black line with various datapoint shapes to indicate the different phases of torpor) increased in the morning as T_a (blue line) increased outside the roost. The active arousal recorded using the definition, described in the Methods in the main text, is shown with different shapes of the points (being a 'Mixed' arousal – see main text for definition – it has one point marked as an entry). The arrow marks the point which would have been recorded as the first datapoint in the arousal had a threshold value of 0.2°C been used, as derived from Utz et al. (2007), instead of 0.6°C. **(b)** The change in T_{skin} from previous measurement (ΔT_{skin}) across the timeline, with the red dashed line indicating the threshold-value 0.6°C used in this study, and the gray line indicating a threshold-value of 0.2°C. Had the latter threshold value been implemented here, the torpor arousal would have been recorded as 2 hours longer in duration than the current 50 minute long registered arousal.

1.2 Sensitivity testing of the general ΔT_{skin} threshold value

To decide on a sensible ΔT_{skin} threshold value to apply to our dataset we looked at the phase-durations (Fig. S1.2a) and the number of phases (Fig. S1.2b) recorded when applying a range of ΔT_{skin} threshold values, from 0.1 up to 1.2, while keeping the 'within bout' requirement value (see section 1.3 below) stable at 1.5. For the general ΔT_{skin} threshold value the sensitivity was stronger for the phase durations than for the number of phases recorded (see Fig. S1.2). Lowering the ΔT_{skin} threshold value led to some reductions in the number of phases being recorded between threshold values, but mainly it led to potentially drastic increases in the durations of each phase, as shown in Fig. S1.2a. We therefore decided on the ΔT_{skin} threshold value mainly by evaluating the changes to phase durations, which seemed to reach a first stabilizing level around value of 0.6 (marked in red in Fig. S1.2).

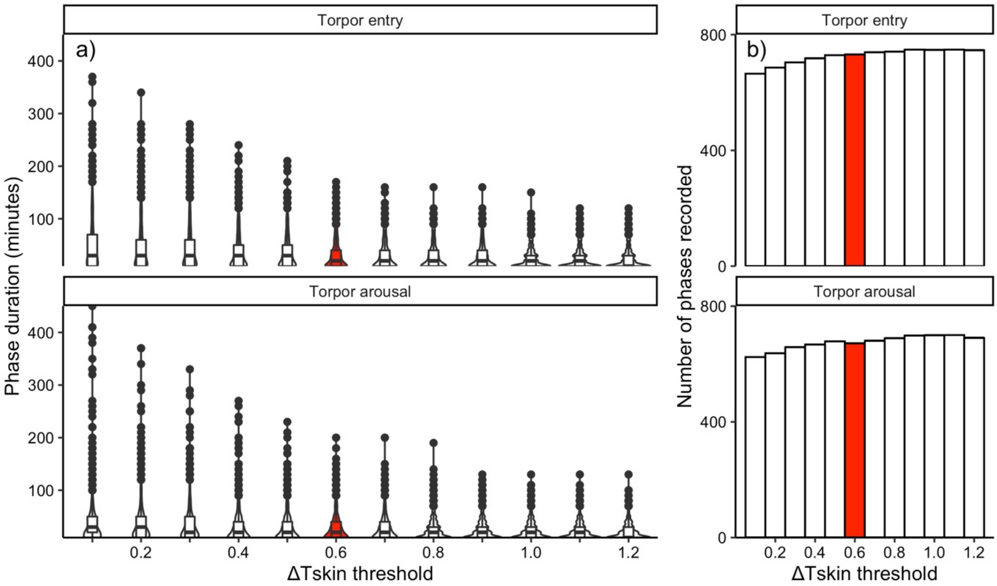


Figure S1.2: Results from applying the method with ΔT_{skin} threshold values ranging from 0.1 to 1.2 (while keeping the 'within bout' ΔT_{skin} requirement stable at 1.6). Based on the phase durations **(a)** and the number of identified phases **(b)** recorded across the ΔT_{skin} threshold range, a ΔT_{skin} threshold value of 0.6 was chosen for our dataset (marked in red in figure). The choice is based upon visual inspection of the first stabilising period in the data.

1.3 Sensitivity testing of the ‘within bout’ ΔT_{skin} requirement value

We chose to implement a requirement value as a criterion for detecting within-bout phases to reduce the risk of classifying passive rewarming- or cooling periods, or even single datapoints, as active phases. For the phases connected to the initial entry or arousal of a torpor bout the identification of the transition across the T_{onset} threshold is a nice criterion for detecting associated torpor phases, but the within-bout phases lack such a distinction and may therefore be more vulnerable to identifying passive phases as active ones. We therefore applied the requirement of at least one ΔT_{skin} value above or below a certain threshold before classifying it as a phase. Similar to the ΔT_{skin} threshold value we decided on a sensible within bout ΔT_{skin} requirement value by testing the recorded phase durations (Fig. S1.3a) and number of phases recorded (Fig. S1.3b) when applying a range of ΔT_{skin} requirement values to the dataset, here between 0.6 up to 2.0. For the within bout ΔT_{skin} requirement value the sensitivity was stronger for the number of phases recorded than for the duration of each phase (see Fig. S1.3), with a lowering of the threshold value leading to potentially drastic increases in the number of phases recorded in the data. This is due to single datapoints above the ΔT_{skin} requirement threshold value being identified as full phases (see medians for lower values in Fig. S1.3a). We did not wish to limit the method to only identifying phases of certain durations (i.e. phases lasting for more than one measurement) as we believe many of these single datapoint within bout phases to be accurately identified. However, we wanted to ensure that such phases were, in more cases than not, included because they were indeed active phases as opposed to passive ones. For the within bout ΔT_{skin} requirement value we therefore decided upon a sensible value mainly by looking at the number of recorded phases across the tested values (Fig. S1.3b and c). The change in number of recorded phases from one value to the next is better illustrated in Fig. S1.3c, indicating a stabilizing period around a ΔT_{skin} value of 1.5. We therefore decided upon a suitable ΔT_{skin} requirement threshold value of 1.5 for our dataset (marked in red in Fig. S1.3).

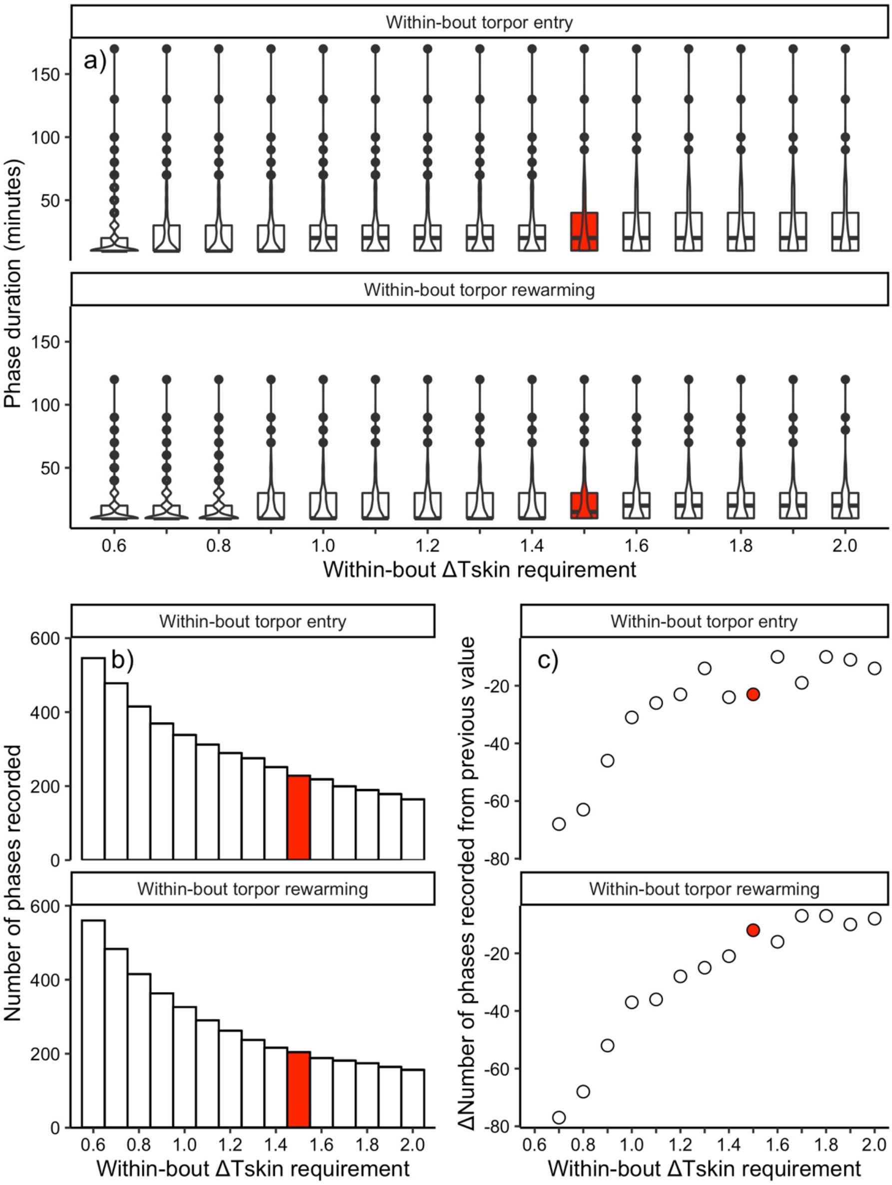
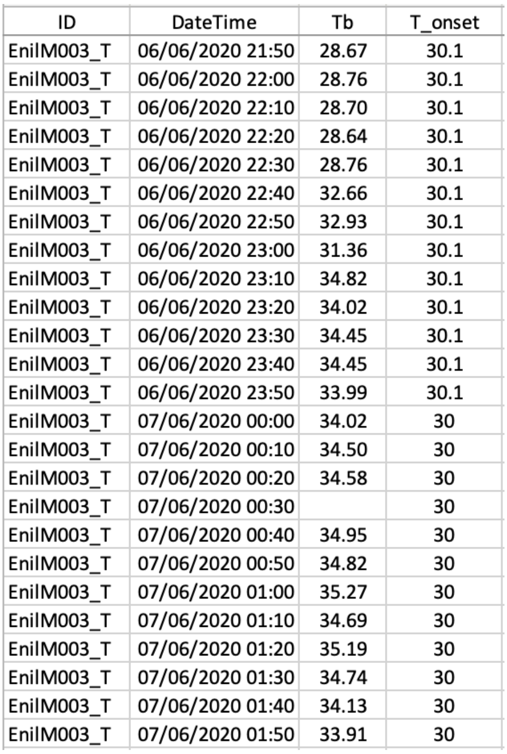


Figure S1.3: Results from applying the method with various ΔT_{skin} requirement values for identifying 'within bout' phases, ranging from 0.6 to 2.0 (while keeping the general ΔT_{skin} threshold stable at 0.6). Based on the phase durations **(a)** and the number of identified phases **(b)** recorded across the ΔT_{skin} threshold range, a ΔT_{skin} threshold value of 1.5 was chosen for our dataset (marked in red in figure). The choice is based upon visual inspection of the first stabilising period in the data.

Supplementary Materials 2: R-code instructions and assumptions

2.1 Example of option 3 (line 74 to 78 in R-script)

If there are multiple T_{onset} values calculated for a dataset (varying between individuals and/or days), a column listing the T_{onset} values should be included before uploading the dataset into R. An example of how such a dataset could look is shown in Figure 2.1.



ID	DateTime	Tb	T_onset
EnilM003_T	06/06/2020 21:50	28.67	30.1
EnilM003_T	06/06/2020 22:00	28.76	30.1
EnilM003_T	06/06/2020 22:10	28.70	30.1
EnilM003_T	06/06/2020 22:20	28.64	30.1
EnilM003_T	06/06/2020 22:30	28.76	30.1
EnilM003_T	06/06/2020 22:40	32.66	30.1
EnilM003_T	06/06/2020 22:50	32.93	30.1
EnilM003_T	06/06/2020 23:00	31.36	30.1
EnilM003_T	06/06/2020 23:10	34.82	30.1
EnilM003_T	06/06/2020 23:20	34.02	30.1
EnilM003_T	06/06/2020 23:30	34.45	30.1
EnilM003_T	06/06/2020 23:40	34.45	30.1
EnilM003_T	06/06/2020 23:50	33.99	30.1
EnilM003_T	07/06/2020 00:00	34.02	30
EnilM003_T	07/06/2020 00:10	34.50	30
EnilM003_T	07/06/2020 00:20	34.58	30
EnilM003_T	07/06/2020 00:30		30
EnilM003_T	07/06/2020 00:40	34.95	30
EnilM003_T	07/06/2020 00:50	34.82	30
EnilM003_T	07/06/2020 01:00	35.27	30
EnilM003_T	07/06/2020 01:10	34.69	30
EnilM003_T	07/06/2020 01:20	35.19	30
EnilM003_T	07/06/2020 01:30	34.74	30
EnilM003_T	07/06/2020 01:40	34.13	30
EnilM003_T	07/06/2020 01:50	33.91	30

Figure S2.1: Example of dataset where the T_{onset} value is calculated for each day within each individual. The T_{onset} values for each row should be included in a column named T_onset before uploading the dataset to R.

2.2 Examples of potential issues or assumption in the R-code output

2.2.1 Complete torpor bouts not identified

In our specific dataset on free-ranging bats, the R-code sometimes did not identify complete torpor bouts due to the bats leaving the roost to forage before their body temperature was recorded to be above the T_{onset}, and as such were not identified with an active arousal but rather with a within-bout arousal. Because a complete torpor bout was determined based on the presence of an entry and an arousal starting or ending above the T_{onset}, these torpor bouts therefore remained un-identified. This was a similar issue for bats returning to the roost that decreased their T_{skin} below the T_{onset} before the next data measurement. Examples of such cases are shown in Figure 2.2. This should only be problematic for datasets similar to our own, where the T_b or T_{skin} measurements are no longer recorded during certain activities like foraging or roost relocation, and where the intervals between recordings are long enough for the animals to rewarm above or cool down below the T_{onset} and leave or return to the (roost) location where it can be measured before the next data logging (Fig. 2.2).

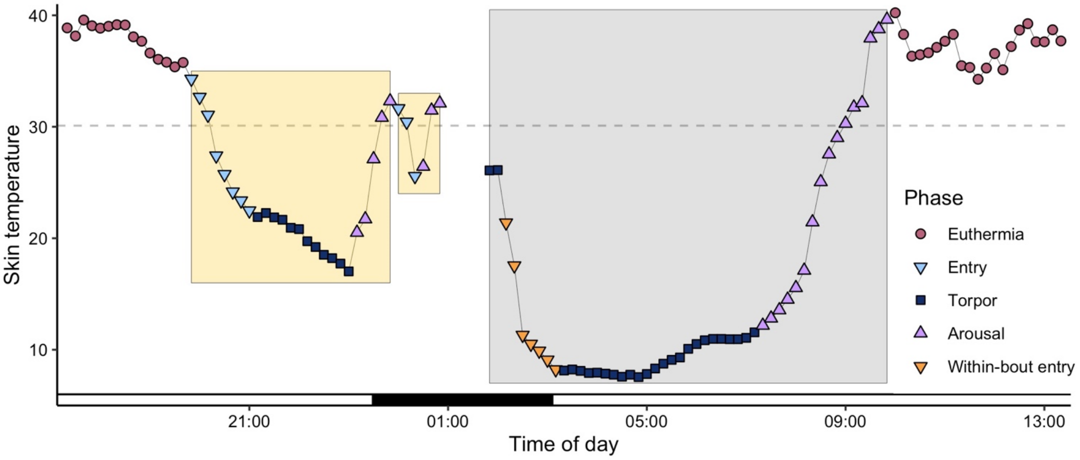


Figure S2.2: Example of skin temperature recorded from a northern bat. Across this timeframe the bat apparently expressed three torpor bouts: the two first torpor bouts were identified (yellow windows), while the third torpor bout was not detected as a complete torpor bout (grey window) due to the first measurement after the bat returned back to the roost after foraging was lower than the T_{onset} (dashed grey line). The torpor entry in this torpor bout was, as such, recorded as a within-bout entry as it did not start above the T_{onset} value. Time between sunset and the following sunrise is indicated by the black horizontal bar on the x-axis.

2.2.2 Back-to-back torpor bouts

In the R-code, we have specified that a complete torpor bout lasts from the first datapoint registered as a torpor entry until the last point of the torpor arousal (not counting within-bout phases). However, occasionally our measured bats would go from arousing above the T_{onset} to immediately enter back into a new torpor period. If the animals are expressing shallow torpor close to the T_{onset}, even small temperature fluctuations may cause the identification of several torpor bouts back-to-back. An example of this is shown in Figure 2.3. For our data we believe that this distinction between torpor bouts is suitable, but as this might be a question of subjectivity, we include it here so that any researcher applying our R-code to their datasets may be aware of this assumption. Back-to-back torpor bouts can be identified in the datasets after applying the R-code by tracing torpor bouts with an ID that is between full numbers (i.e. 1.1, 1.2 etc. as opposed to 1, 2 etc.).

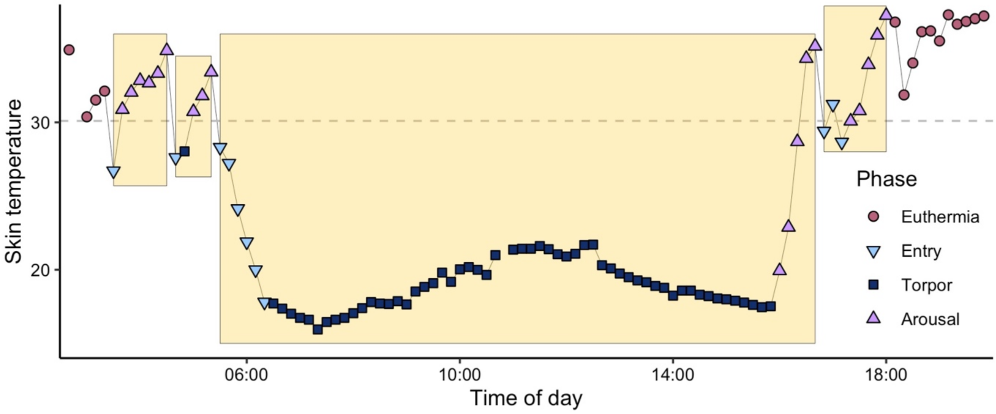


Figure S2.3: Example of skin temperature recorded from a brown long-eared bat. Here our method identified four consecutive and complete torpor bouts (indicated by the yellow windows).

Paper IV

The small-bat-in-summer paradigm: energetics and adaptive behavioural routines of bats investigated through a stochastic dynamic model

Mari Aas Fjelldal[1]*, Amandine Sophie Muller[1], Irja Ida Ratikainen[1], Clare Stawski[1,2] & Jonathan Wright[1]

[1]Department of Biology, Norwegian University of Science and Technology (NTNU), 7491 Trondheim, Norway
[2]School of Science, Technology and Engineering, University of the Sunshine Coast (USC), Maroochydore DC, Queensland, 4558, Australia

Abstract

Strong seasonality at high latitudes represents a major challenge for many endotherms as they must balance survival and reproduction in an environment that varies widely in food availability and temperature. Being heterotherms, bats spend long cold winters in hibernation, avoiding the challenges faced by many animals. To avoid energetic mismatches caused by limited foraging time and stochastic weather conditions, bats can also employ this energy-saving state of torpor during summer to save accumulated energy reserves. However, at high latitudes small-bats-in-summer face a particular challenge: as nocturnal foragers they rely on the darkness of the night to avoid predators and/or interspecific competition, but for many the summer involves short nights of mostly twilight, and even a lack of true night at the northernmost distributions of some bat species. To investigate optimal individual behaviour across diurnal cycles, we constructed a stochastic dynamic model of bats living at high latitudes. Using a detailed parameterized model framework with values that are representative for our study system, we show that individual energetic reserves are a strong driver of day-time use of torpor and night-time foraging behaviour alike, with these linked effects being both temperature and photoperiod dependent. We further used the model framework to predict survival probabilities at five locations across a latitudinal gradient (60.1°N to 70.9°N), finding that photoperiod is the main limiting factor to bat species distributions. To verify the accuracy of our model results, we compared predictions for optimal decisions with our own empirical data collected on northern bats (*Eptesicus nilssonii*) from two latitudes in Norway. The similarities between our predictions and observations provide strong confirmation that this model framework incorporates the most important drivers of diurnal decision-making in bat physiology and behaviour. Our model findings regarding state-dependent decisions in bats should therefore contribute to the understanding of how bats cope with the summer challenges at high latitudes.

Key words: Small bird in winter, heterothermy, dynamic programming, torpor, state dependent, diurnal routines, thermal physiology

Introduction

The dilemma of small-birds-in-winter needing to balance high energetic demands with limited foraging opportunities during short winter days is a well-known paradigm in behavioural ecology research (e.g. Bednekoff & Houston 1994; McNamara *et al.* 1994; Brodin 2007; Brodin *et al.* 2017). A similar but less well known dilemma is the one small bats face in summer. At northern latitudes the summer seasons are short, with only a few months available for the bats to reproduce and build up sufficient fat reserves to survive the subsequent long and cold winter in hibernation. The northern summer season is characterised by short nights consisting largely of periods of twilight, which limit the time nocturnal creatures like bats have available to forage in safety from aerial predators (Speakman *et al.* 2000). Furthermore, most temperate zone bat species are insectivorous, and therefore dependent upon a food source that constantly fluctuates with environmental conditions, such as temperature and precipitation (see Taylor 1963; Speakman *et al.* 2000). Being the only mammals in the world capable of powered flight, bats also have a high energy expenditure during each foraging trip (Winter & Von Helversen 1998). Consequently, when summer nights are short and weather conditions are poor, bats may face a mismatch between the energy expenditure needed for flight and the amount of available prey when foraging, which potentially limits the northern range of many bat species (Parker *et al.* 1997).

One way for insectivorous bats to overcome these energetic challenges of summer foraging is to use the energy-saving state of torpor during day-time or on nights when foraging prospects are poor (Ruf & Geiser 2015). Torpor is characterised by a controlled and reversible reduction in heart rate and oxygen consumption while temporarily abandoning the defence of a high and stable body temperature (Geiser 2021). Due to its inherent potential for saving large amounts of energy, temporal heterothermy is an important evolutionary trait that in the short-term may enhance individual survival and in the long-term reduce the risk of species extinctions (Geiser & Turbill 2009; Liow *et al.* 2009; Stawski *et al.* 2014). However, despite the apparent benefits of torpor (and hibernation) as an energy-saving state during inclement conditions, there are some inherent costs that will influence any adaptive state- and weather-dependent use of torpor. Firstly, employing torpor may help save energy, but rewarming from torpor brings associated energetic and physiological costs that may limit the energetic benefit (Currie *et al.* 2015; Landes *et al.* 2020). Detrimental physiological costs of prolonged hibernation periods have also been identified (Humphries *et al.* 2003; Boyles *et al.* 2020), but these were found to be reversible following frequent arousals (Humphries *et al.* 2003). Such costs should therefore be less likely to affect the expression of daily torpor in non-reproductive bats outside of the hibernation season. Secondly, and perhaps more importantly for the individual bat during summer, are the potential benefits of being awake. Most bat species are highly social and dependent upon frequent interactions with roost mates to obtain important benefits like social grooming, cooperative offspring care, sharing of information or attracting mates (Wilkinson *et al.* 2016; Chaverri *et al.* 2018). Bats strategically choose warm roosts during summer to facilitate lower thermoregulatory costs of being awake, which is important particularly for pregnant or lactating females as they face added costs to their reproduction if they employ frequent deep torpor bouts (Speakman & Rowland 1999; Lausen & Barclay 2003; Lourenço & Palmeirim 2004). Non-reproductive and post-lactating individuals may also spend considerable periods of time awake during day- and night-time in summer, although the expression of torpor is found to vary greatly with weather and roost type (Lausen & Barclay 2003; Bergeson *et al.* 2021; Fjelldal *et al.* 2021).

Even in non-reproductive bats, there is likely to be a complex relationship between the optimal energetic decision to use torpor versus being awake in the roost (henceforth referred to as *resting*) or foraging outside. Environmental temperature has been identified as a strong driver of general bat behaviour (e.g. see Ruf & Geiser 2015), but body mass have also been found to impact individual strategies such as summer night-time torpor use (Fjelldal *et al.* 2021) and microclimate selection during winter hibernation (Boyles *et al.* 2007). Indeed, the effect of within-individual variation in body mass (i.e. fat reserves and stomach contents) on daily decision making in bats is largely unstudied due to the challenges of continuous monitoring of free-ranging individuals, making this an appropriate moment to fully explore our theoretical expectations.

This study therefore presents one of the first theoretical models for understanding individual optimal state-dependent decisions in daily heterotherms like bats. Our stochastic dynamic optimization model is developed using detailed parameterisation from natural systems in order to quantitatively predict optimal behaviour as accurately as possible. By incorporating quantified values such as dynamic photoperiods, light- and state-dependent predation risk, representative daily temperature conditions for the roost and outside air, temperature-dependent prey availabilities and physiological costs of different activities, our model includes all of the variables we consider likely to be important drivers of behaviour and thermal physiology in non-reproductive bats. The model organism here is based upon physiological data collected from the literature on various species of insectivorous small-bodied bats (see Supplementary Materials 1). Physiological energetics in bats depend upon body mass and temperature, but show no apparent latitudinal or climate zone effects of local adaptation (Speakman & Thomas 2003; Skåra *et al.* 2021; Fjelldal *et al.* 2022). Our model organism should therefore be representative of any small-bodied insectivorous bat species inhabiting seasonal environments. To test the applicability of our model predictions, we briefly compare the model results with empirical data collected on northern bats (*Eptesicus nilssonii*) at two latitudes in Norway (Nittedal, 60.1°N and Trondheim, 63.4°N). Our study aims are three-fold. Firstly, we seek to discover how bats at the northern limits of their species distributional range overcome the associated challenges of summer survival through the strategic use of torpor. Secondly, we want to explore the magnitude of state-dependency on this behavioural and thermal physiological decision-making employed across a range of climatic conditions. Finally, by running model simulations of one month summer survival across a large latitudinal gradient, we attempt to determine the main limiting causes of bat species distributional ranges at their northern limits. Through our findings, we aim to provide a deeper understanding of the diurnal nature of strategic decision-making by bats, and thus their scope for adaptation to changing environments.

Methods

Stochastic dynamic programming

We used stochastic dynamic programming (see Houston *et al.* 1988; Clark & Mangel 2000) to investigate the optimal sequence of state-dependent decisions made by small bats in summer. The model time horizon (T) consisted of 72 daily timesteps (t) repeated for 30 days (D), thus focusing on the life of small bats through the lightest summer month of the year. As we wanted to investigate the impact of behavioural and physiological decisions on individual energetics for non-breeding bats in summer, we allowed the three following behaviours for the bats to choose from:

1. Torpor – bat in the roost, torpid
2. Resting – bat in the roost, awake
3. Foraging – bat outside of the roost, foraging

Parametrization

The parametrization was developed by collecting biologically relevant values from the literature for the physiological parameters (see Supplementary Materials 1). For the different environmental scenarios, we used temperature data obtained through the Norwegian Centre for Climate Services and our own light-measurements at two high-latitude field sites: Nittedal, Norway (60.1°N, 10.8°E) and Trondheim, Norway (63.4°N, 10.4°E). The light-measurements were used to estimate a light-dependent predation threat variable and a light-dependent energetic competition cost (i.e. we assume variation in fitness costs like predation threat, interspecific competition for food and mobbing by non-competitor species to be determined by light conditions and energy reserves, see below). Baseline parameter values for our stochastic dynamic models are shown in Table 1a and Table 1b, comparing two locations that differ in latitude and therefore in light-conditions and the associated predation threats and competition costs. The values represent average conditions for the month of July in Nittedal and Trondheim, thus representing one of the months with the shortest nights and the lightest twilight at these high-latitude locations.

Environmental conditions like temperature and perceived predation threat (based on sunlight illumination-levels) are non-static across the daily cycle in the natural systems we base our model upon. Therefore, we implemented time- or temperature-dependent variables when appropriate in order to capture the dynamic diurnal environments experienced by individuals at specific latitudes and times of year. Figure 1 shows the dynamic values of the baseline parametrizations, where time-dependent variables show fluctuations between sunrise ($t = 1$) and the following sunrise ($t = 1$ next day). Based upon meteorological data from Norwegian Centre for Climate Services, we specified six daily weather types as shown in Figure 1a: 'very warm days' (mean daily temperatures > 20°C and daily maximum temperatures > 26°C), 'dynamic warm days' (mean daily temperatures > 14°C and daily temperature ranges ≥ 6°C), 'stable warm days' (mean daily temperatures > 14°C and daily temperature ranges < 6°C), 'dynamic cold days' (mean daily temperatures ≤ 14°C and daily temperature ranges ≥ 3°C), 'stable cold days' (mean daily temperatures ≤ 14°C and daily temperature ranges < 3°C), and 'very cold days' (mean daily temperatures < 9°C, minimum daily temperature < 6°C and maximum daily temperature < 13°C), with a probability (p_w) for the occurrence of each weather condition event. The different daily temperature cycles in the roost (Fig. 1a, dashed lines) were estimated using our own collected field-data (see Supplementary Materials 1), which further impact metabolic costs (Fig. 1b), while outside air temperatures (Fig. 1a, solid lines) affect prey availabilities (Fig. 1c). For simplicity, the estimated predation threat and competition cost in the model did not differentiate between day types (Fig. 1d), but we added a slight increase in predation threat with level of energy reserves in line with published estimates of mass-dependent flight costs (Anthony & Kunz 1977; Aldridge 1987; Witter & Cuthill 1993), which broadly tally with observations of heavy individual bats being more light avoiding (Speakman 1991b). We thus specify a simple pattern of light-dependent predation threat from avian diurnal raptors and an interspecific competition cost to test if this is sufficient to generate realistic diurnal activity patterns in our model bat. We included two types of costs since the origins of the evolution of nocturnal activity in bats are currently unclear, potentially being related to niche-differentiation, mobbing or risk of hyperthermia, as well as diurnal predation threat (Rydell & Speakman 1995; Speakman 1995; Speakman *et al.* 2000).

Table 1a: General parameter definitions and model baseline values. Details and justifications for the parameterization can be found in Supplementary Materials 1, including equations for the air temperature cycles across day types. Text in bold indicate when values differ between locations.

Symbol	Parameter	Values	Main reference
D	Number of days in month	30	Model structure
T	Number of timesteps in month	2160 (72 × 30)	Model structure
X_0	Mass of bat with no fat reserves	7 g	Model assumption
X_{max}	Max body fat deposit	3 g (40 discrete steps)	Model assumption
X_{min}	Fat reserve threshold for survival	0.05 g	Model assumption
X_{dec}	Threshold for decreasing survival	2 g	Model assumption
Y_{state}	Temperature state	*Torpid* or *Non-torpid*	Model structure
tnz	Thermal neutral zone	≥ 29°C	Geiser and Brigham (2000)
w	Weather type across 24 hours	Very warm, dynamic warm, stable warm, dynamic cold, stable cold, very cold	Model structure
$\text{air}_{\text{\_very\_warm}}(t)$	Temperature outside, very warm day	Equation S1.5	Norwegian Centre for Climate Services (NCCS)
$\text{air}_{\text{\_dynamic\_warm}}(t)$	Temperature outside, dynamic warm day	Equation S1.6	NCCS
$\text{air}_{\text{\_stable\_warm}}(t)$	Temperature outside, stable warm day	Equation S1.7	NCCS
$\text{air}_{\text{\_dynamic\_cold}}(t)$	Temperature outside, dynamic cold day	Equation S1.8	NCCS
$\text{air}_{\text{\_stable\_cold}}(t)$	Temperature outside, stable cold day	Equation S1.9	NCCS
$\text{air}_{\text{\_very\_cold}}(t)$	Temperature outside, very cold day	Equation S1.10	NCCS
$\text{roost}_{\text{\_warm}}(\text{air}(w,t), t)$	Temperature roost, warm day types	$\text{air}(w,t) + (2.34 + 0.27 \times t - 2.75 \times 10^{-4} \times t\text{^}2 - 4.88 \times 10^{-5} \times t\text{^}3)$	Own data
$\text{roost}_{\text{\_cold}}(\text{air}(w,t))$	Temperature roost, cold day types	$\text{air}(w,t)$ + 2°C	Own data
p_w	Probability of very warm days, dynamic warm days, stable warm days, dynamic cold days, stable cold days, and very cold days, respectively	**For Nittedal**: 0.24, 0.48, 0.07, 0.20, 0.01, 0 **For Trondheim**: 0.13, 0.30, 0.04, 0.47, 0.04, 0.02	NCCS

Table 1b: Parameter definitions and model baseline values for each behaviour. Equations for the temporal predation threats and energetic competition costs can be found in Supplementary Materials 1.

Symbol	Parameter	Values	Main reference
Behaviour 1 (torpor)			
$\lambda(\mathrm{air}(w,t))$	Food availability	0	Model assumption
$\mu(\mathrm{t})$	Predation threat baseline	0	Model assumption
$C_{TMR}(\mathrm{roost}(w,t))$	Hourly cost of TMR	$0.0008 \times \exp(0.086 \times \mathrm{roost}(w,t) \times X_0)$ if $C_{TMR} < C_{BMR} \times 0.9$; $C_{BMR} \times 0.9$ if $C_{TMR} \geq C_{BMR} \times 0.9$	Fjelldal *et al.* (2022)*
$C_{RW}(\mathrm{roost}(w,t))$	Rewarming cost	$0.018 - 0.00046 \times \mathrm{roost}(w,t) \times X_0$	Turbill (2008)*
Behaviour 2 (resting)			
$\lambda(\mathrm{air}(w,t))$	Food availability	0	Model assumption
$\mu(\mathrm{t})$	Predation threat baseline	0	Model assumption
C_{BMR}	Hourly BMR cost (for roost ≥ tnz)	$0.0052\ \mathrm{g} \times X_0$	Geiser and Brigham (2000)*
$C_{RMR}(\mathrm{roost}(w,t))$	Hourly RMR cost (for roost < tnz)	$0.036\ \mathrm{g} \times X_0 - 0.0011 \times \mathrm{roost}(w,t) \times X_0$	Geiser and Brigham (2000)*
θ	Resting fitness benefit	0.0015	Model assumption
Behaviour 3 (foraging)			
α	Potential energy gain per hour	1.3 g	Søraås *et al.* (2022)*
$\lambda(\mathrm{air}(w,t))$	Food availability	$\alpha / (1 + \exp(-0.52 \times (\mathrm{air}(w,t) - 8))$	Speakman *et al.* (2000)*
κ	Coefficient for energy reserve effect on foraging success	-0.03	Model assumption
$p_{food}(x)$	Probability of finding available food	$0.9*\exp(\kappa(x))$	Model assumption
$\mu(t)$	Predation threat baseline	0.0001 if $\mu < 0.0001$ & 0.2 if $\mu > 0.2$; **For Nittedal:** Equation S1.13 if $0.0001 \leq \mu \leq 0.2$ **For Trondheim:** Equation S1.14 if $0.0001 \leq \mu \leq 0.2$	Own data
r	Coefficient for energy reserve effect on predation threat	0.05	Model assumption
$C_{competition}\ (t)$	Energetic competition cost	0.0001 if $C_{competition} < 0.0001$ & 0.2 if $C_{competition} > 0.2$; **For Nittedal:** Equation S1.19 if $0.0001 \leq C_{competition} \leq 0.2$ **For Trondheim:** Equation S1.20 if $0.0001 \leq C_{competition} \leq 0.2$	Own data
C_{flight}	Hourly flight cost	0.615 g	Kurta *et al.* (1989)*

* Converted from original values, see Supplementary Materials 1

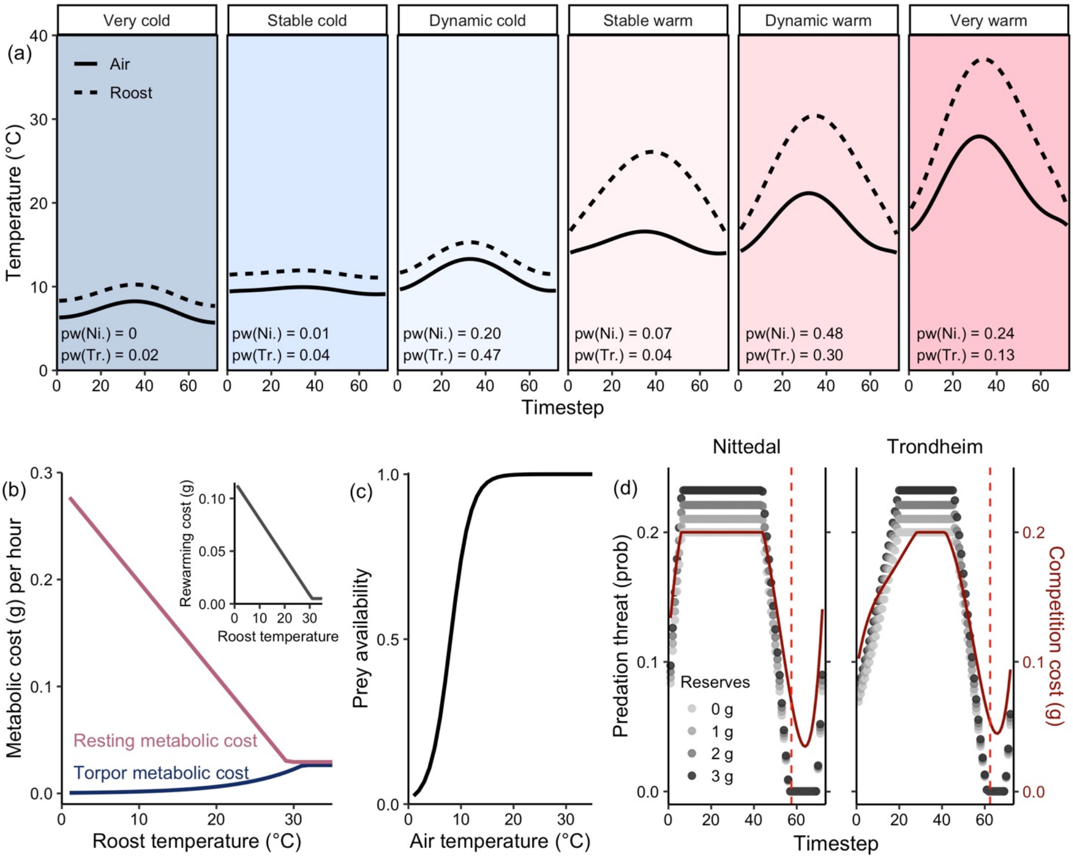


Figure 1: The dynamic parameter values used in the model (for the non-dynamic parameter values, see Table 1a and Table 1b). **(a)** Diurnal temperature fluctuations across six different day types for the outside air (solid lines, which impacts the insect abundance), and inside the roost (dashed lines, which affects the metabolic costs of resting, employing torpor and rewarming from torpor). p_w indicates the occurrence probability of each day type in Nittedal (denoted with Ni.) and Trondheim (denoted with Tr.) **(b)** Hourly metabolic costs shown as grams of energy reserves for behaviour 1 (torpor; dark blue line) and 2 (resting; dark pink line) as a function of roost-temperature. The smaller inset plot shows the linear function of the total rewarming cost against roost-temperature when transitioning from the state ‘torpid’ to the state ‘non-torpid’. **(c)** Prey availability as a function of the outside air temperature. **(d)** Diurnal variation in predation threat (grey-scale points) and energetic competition cost (dark red solid lines) calculated from light-measurements at the two locations Nittedal and Trondheim (see Supplementary Materials 1). The grey-scale indicates state-dependent (i.e. body mass) effects on predation threat, with individual energy reserves increasing from 0 to 3, and heavier individuals experiencing increased threat of predation. Dashed vertical red lines indicate timing of sunset at each of the two locations.

Model construction

The models were developed in R (version 4.0.3) and consist of two parts: a 'backwards' calculation of the optimal behaviour in each instance, in which we calculate the fitness of a hypothetical individual at a given time-of-day and physiological state across a wide range of possible scenarios; followed by a 'forward' iteration that simulates the best individual sets of diurnal sequences of these optimal decisions (see Clark & Mangel 2000). R-codes for the model are included as r-scripts in the Supplementary Materials. For our model framework, we used survival probability as the fitness proxy that the bats would attempt to maximize across the time horizon. The dynamic programming functions for our small bat in summer model were thus based on optimizing survival, $V(x, y, w, t, d)$ (see equations 1 to 7 below), this being the maximum probability for a bat to survive from time period t until the last time period of the summer (T, D) plus their expected future fitness after summer $S(x)$. Here, X represents the energetic state in terms of potential energy reserves with the current value x, Y is the body temperature state with the current state denoted as y, and W is the weather conditions with the current condition w. Therefore, X and Y function as the two individual state variables that are impacted by, as well as driving, individual decisions, while W represents the stochastic element of the model that affects costs and benefits associated with the different decisions.

In the model, bats can optimise their fitness by choosing between three activities (a): (1) employing torpor in the roost; (2) resting in the roost; or (3) foraging outside of the roost. The first two options have an associated predation threat of 0, but no food intake (Table 1b). The foraging option included a temperature-dependent food availability ($\lambda(\mathrm{air}(w,t))$, Table 1b, Fig. 1c), but this activity also involved a predation threat and an energetic competition cost that varied across the daily cycle (Table 1b, Fig. 1d). We implemented an accelerating mass-dependent predation risk ($\mu(t)^{rx}$), as well as declining foraging success with increasing individual fat deposits ($p_{food}(x)$), because we expect increasing flight costs and less agility in bats as individual body mass increases (Anthony & Kunz 1977; Aldridge 1987).

The two non-foraging activities, torpor and resting, differed in their respective temperature-dependent physiological costs (Fig. 1b). In our model, torpid individuals decreased their energy expenditure dramatically at low temperatures compared to resting individuals. However, the difference between the energetic costs decreased with increasing temperatures, until the curves flattened at a parallel level of torpor metabolic rate (TMR) being 90% of basal metabolic rate (BMR). Thus, a bat would at any temperature spend less energy employing torpor than resting, but the energetic benefit of torpor would decrease with increasing temperatures. In addition, we implemented a temperature-dependent cost of arousing from torpor (Fig. 1b), which was paid when an individual transitioned from the state 'torpid' to the state 'non-torpid'. We expect there to be other potential associated physiological or ecological costs of prolonged periods spent in torpor (Humphries *et al.* 2003), but potential benefits of being awake might be more important to the individual bat during summer. We therefore implemented a fitness-benefit (θ) per time interval for resting activity versus being in torpor, which from our findings below we believe is an important aspect of the model and probably the natural world alike, although it has yet to be quantified in empirical studies.

The programming function is defined as:

$$V(x, y, w, t, d) = \max_a [H(x, y, w, t, d, a)] \,, \tag{1}$$

$$\text{if } t < 72\text{: } H(x, y, w, t, d, a) = \theta_\alpha + S(X) \times (1-\mu(t,x)) \times \\ (E_a[V(x'_{food}, y', w, t+1, d)] \times p_{food,a(x)} + \\ E_a[V(x'_{no\ food}, y', w, t+1, d)] \times (1 - p_{food,a(x)})) \,, \tag{2}$$

$$\text{if } t = 72\text{: } H(x, y, w, 72, d, a) = \theta_\alpha + S(X) \times (1-\mu(t,x)) \times$$

$$\sum_{w=1}^{6} p_w \times \left(E_a\left[V\left(x'_{food}, y', w, t=1, d+1\right)\right] \times p_{food,a(x)} + E_a\left[V\left(x'_{no\,food}, y', w, t=1, d+1\right)\right] \times \left(1 - p_{food,a(x)}\right)\right) , \tag{3}$$

$$x'_{food} = x - C_a(t,w) - C_{RW}(y,a,t,w) + \lambda(t,w) , \tag{4}$$

$$x'_{no\,food} = x - C_a(t,w) - C_{RW}(y,a,t,w) , \tag{5}$$

$$C_a(t,w) = \begin{cases} C_{TMR}(t,w) \text{ if } a = 1 \\ C_{BMR} \text{ if } a = 2 \text{ and } T_{roost} \geq TNZ \\ C_{RMR}(t,w) \text{ if } a = 2 \text{ and } T_{roost} < TNZ \\ C_{flight} \text{ if } a = 3 \end{cases} . \tag{6}$$

Each day (*d*) with its 72 timesteps (each *t* corresponding to 20 minutes) represented a daily cycle starting at sunrise and ending at the following sunrise. This daily cycle was chosen with regard to the nocturnal lifestyle of most bats, modelling a continuous timeline across 24-hours as we were interested in individual-level decisions during both day-time and night-time. We implemented a lower threshold value for energy reserves (X_{min}), where individuals were treated as 'dead' and received no fitness if their energy reserves fell below the threshold at any point. We also applied a linearly decreasing survival probability below a given level of fat deposits (X_{dec}). We thus defined the general survival probability ($S(x)$) of bats as:

$$S(x) = F(x,T,D) = \begin{cases} 1 \text{ if } x \geq X_{dec} \\ \frac{x - X_{min}}{X_{dec} - X_{min}} \text{ if } X_{dec} > x \geq X_{min} \\ 0 \text{ if } x < X_{min} \end{cases} \tag{7}$$

This was true for every *t* and therefore also functioned as the terminal reward ($F(x,T,D)$) in the model. As the end of July is still a long time before the onset of the hibernation season, we did not specify any additional requirement (i.e. above that needed for immediate survival) for over-winter energy reserves to be reached by the end of the time horizon. When energy reserves were between the pre-calculated discrete values, we used linear interpolation to calculate the corresponding fitness value as described in Clark and Mangel (2000) (see details in Supplementary Materials 2).

The optimal decision by the bat of which of the three activities (*a*) to carry out was calculated for every possible fat state (*x*), thermal state (*y*), weather (*w*) and timestep (*t*) within day (*d*), by going 'backwards' from the last time step modelled (*T*). These were saved and used for the 'forward' simulation of optimal sequence of individual behavioural routines for the whole month. For the forward simulations, we simulated 200 bats each starting in the non-torpid state with 1.5 grams of energy reserves at the first timestep in the model. The sequence of day types was randomised across the 30 days with the probability p_w, with a new sequence generated for each simulated individual. Predation threat was included as a stochastic risk in the forward simulations, where individuals that experienced being predated upon were given a new and final energy state of -1, marking them as 'dead'. Another stochastic elements in the forward simulation was the probability of finding food (p_{food}), with a current foraging success of 0 if not successful.

Empirical data comparisons

To test the qualitative and quantitative accuracy of our model predictions, we compared the model forward simulation results with our own data collected on northern bats at two locations in Norway: Nittedal and Trondheim. We used data collected from 7 non-reproductive northern bats in Trondheim

(June 2020: 2; June 2021: 2; July 2021: 3) and on 2 in Nittedal (June 2019: 1, June 2021: 1). Permits to conduct the research were granted by the Norwegian Food Safety Authority (FOTS ID 23284) and the Norwegian Environment Agency (ref. 2018/4899).

Bats at each location were captured using mist-nets set up along tree-corridors and forest openings. Upon capture, individuals were weighed and fitted with a small transmitter (~ 0.5 g, PIP31, Lotek Wireless Inc., Dorset, U.K.) that had been calibrated in a water bath (0°C to 45°C with stepwise increases of 5°C) prior to capture. We attached the tag by trimming a patch of fur from the dorsal region and applying a skin adhesive (B-530 Adhere Adhesive) on the transmitter before attaching it on the bat. The bats were thereafter released and tracked to their day-roosts using radiotelemetry. At the roosts, we put up remote loggers to record pulse-intervals from the transmitters every 10 minutes, which could afterwards be converted to skin temperatures (T_{skin}) based upon the transmitter calibration.

To identify torpor bouts, we applied the method described in Fjelldal *et al*. (2023). This method consists of first determining a torpor onset (T_{onset}) temperature value before differentiating each torpor bout into the three different phases of 'torpor entry', 'stable torpor' periods and 'rewarming'. We therefore first calculated a species-specific T_{onset} value using the following equation (8), which was introduced by Willis (2007):

$$T_{onset} - 1SE = (0.041) \times \text{Body mass} + (0.040) \times T_a + 31.083 \qquad (8)$$

We used the mean values for body mass (mean capture weight: 8.7g ± 0.9) and environmental temperature (T_a; collected by placing temperature-sensitive dataloggers outside each day roost) to calculate a species-specific T_{onset} value. Equation 4 is based upon true body temperature (T_b) recordings with internal sensors, and as $T_b - T_{skin}$ measurements usually is < 2ºC for small mammals (Audet & Thomas 1996; Barclay *et al.* 1996) we extracted 2 degrees from our T_{onset} value to get a torpor T_{skin} threshold value of 30.1ºC. We then extended the torpor bouts to include the full torpor entry and rewarming based upon the criteria described in Fjelldal *et al.* (2023). Bats with $T_{skin} < 30.1$ºC or in the torpor entry or rewarming phase were considered to be *torpid.* Bats in their roost with $T_{skin} \geq 30.1$ºC and not in the torpor entry or rewarming phase were considered to be *resting*, and bats that were away from the roost (detected as a period of time with loss of the transmitter-signal) were considered to be *foraging*. These simplifications of behaviour were used to compare empirical results more easily with the simulated individual model sequences. Using the criteria for each of the six day types we categorized the days and nights (using the whole 24-hour temperature cycle also when determining nights) of the collected data. Sample sizes for each location were: $N_{night} = 31$ (7 'very warm', 7 'dynamic warm', 9 'stable warm', 5 'dynamic cold' and 3 'stable cold') and $N_{day} = 32$ (12 'very warm', 13 'dynamic warm', 3 'stable warm', 4 'dynamic cold') in Trondheim, and $N_{night} = 7$ (5 'dynamic warm', 1 'dynamic cold' and 1 'stable cold') and $N_{day} = 7$ (5 'dynamic warm', 1 'dynamic cold' and 1 'stable cold') in Nittedal.

Based upon the sample sizes from each day type at the two locations, we ran simulations for each location with the same number of simulated individuals for each day type as listed above to compare with the empirical data. We then calculated the percentage of time spent on each of the three behaviours during the day (between sunrise and sunset) and night (between sunset and sunrise) for both simulated individuals and from the field data. The means of day-time or night-time percentages of expressed behaviour for empirical data and model simulations were then compared for each of the two locations using Welch two sample t-tests.

Model predictions across a latitudinal gradient

To investigate limitations to bat species distributions at high latitudes, we calculated optimal decisions and simulated survival for 200 individuals throughout one summer month (30 days) at five locations across a latitudinal gradient: Nittedal (60.1°N), Trondheim (63.4°N), Bodø (67.3°N), Tromsø (69.6°N) and Gamvik (70.9°N). There are no observations of bats above 69.73°N in Norway (GBIF.org), and the northernmost location was therefore included to explore how the model predicted behaviour and survival at an extreme latitude. The only differences between the different location scenarios were probabilities of different day types, daily predation threat cycles and energetic competition cost cycles (see Supplementary Materials 1). For the predation-threat and energetic competition costs for Bodø, Tromsø and Gamvik, where we did not have our own collected light-levels, we used sun altitude obtained from the webpage of SunCalc to estimate light-levels based upon our collected data from Trondheim and Nittedal.

Results

General model simulation results

The final values in the baseline models for Nittedal and Trondheim were a mix of *a priori* estimates from the literature (metabolic costs, flight cost and the cost of arousing from torpor) and systematically tested values for parameters that have not been properly quantified (resting benefit, predation threat, energetic competition cost). Figures S3.1 to S3.11 in Supplementary Materials 3 show the outcome from the various model runs and subsequent simulations of individual decision-making (torpor, resting or foraging) across the daily cycle from sunrise to sunrise for each day type. This shows the results of systematic adjustments in resting benefits (θ), predation threats (μ) and competition costs ($C_{competition}$) around their most likely values. Summarising across all individual iterations for each day-type, the middle panes in the figures thus represent the simulation outcome of baseline values from the model (Table 1a and Table 1b). Increasing or decreasing these values produce less biologically realistic diurnal patterns, as shown in the other panes of each figure. More details are given in Supplementary Materials 3.

The naturalistic diurnal scenario generated by the baseline parameter values was used to model the forward iterations, which reassuringly showed clear diurnal patterns in torpor, resting and foraging for small bats in summer across day types (Fig. 2). We modelled two main scenarios: one representing a low latitudinal (in this comparison) bat population from Nittedal and one representing a high latitudinal bat population from Trondheim. Before sunset on warm day types ($t < 58$ in Nittedal and $t < 62$ in Trondheim), most bats employed torpor in the morning (except bats in Nittedal on 'very warm' days, which most were awake and resting in the morning) and rewarmed to spend various amounts of time resting throughout the day, depending on day type and location (Fig. 2). In Trondheim on 'stable warm' and 'dynamic warm' days, most bats spent the middle of the day resting in their roost before re-entering torpor again in the afternoon. On 'very warm' days in Trondheim and on 'stable warm' and 'dynamic warm' days in Nittedal, most bats stayed awake and resting throughout the afternoon without re-entering torpor before leaving the roost to forage. These two decision patterns (employing torpor in the morning and afternoon with a resting period in the middle, or resting throughout the afternoon after a morning torpor bout) are the two most common daily torpor cycles found in free-ranging bats outside of the hibernation season, and are observed in bat species across climate zones (Fjelldal *et al.* 2022). During cold day types, the simulated bats spent the whole day torpid at both locations, and most of the bats even spent the whole night in the torpid state (Fig. 2). This daily pattern of spending the full day and following night torpid has been observed in several studies on various bat species, and is the second most frequently observed pattern in high-latitude northern bats (Fjelldal *et al.* 2022). Between sunset and the following sunrise during warm day types, however, simulated bats spent varying amounts of time foraging, resting and employing torpor, depending on day type and location (Fig. 2).

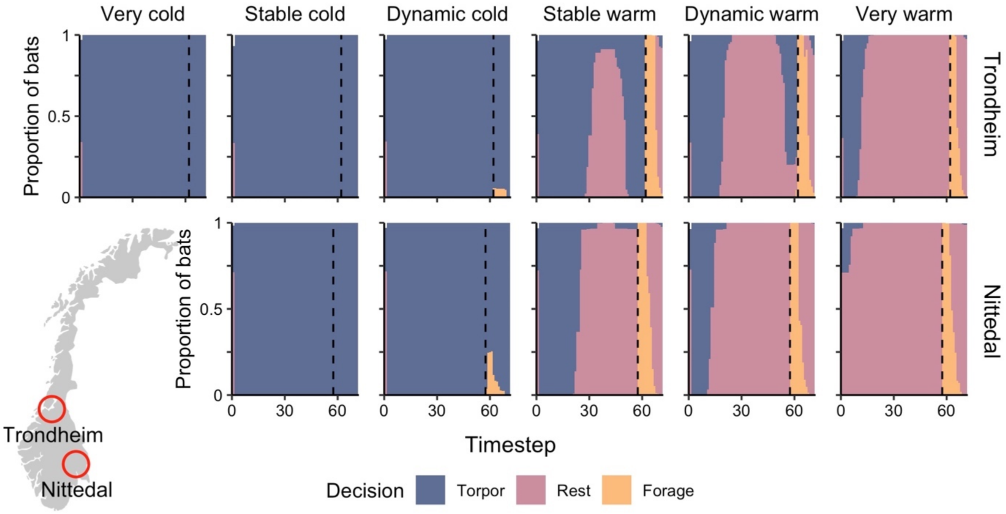


Figure 2: Frequency plots of the individual activities across the daily cycle (from sunrise to following sunrise) for different day types at the two locations Nittedal (lower panes) and Trondheim (upper panes). The plots summarise the decisions at each timestep made by 200 simulation forward model runs (individuals) across 30 days for each of the two locations. The bats could choose between employing torpor (blue), resting (pink) and foraging (yellow) at each timestep. Vertical dashed lines indicate the timing of sunset (at $t = 58$ in Nittedal and $t = 62$ in Trondheim). 'Very cold' day types are not shown for the Nittedal location because such days were never recorded during July in Nittedal and thus had an occurrence probability of 0 in the model.

The fluctuations in energy reserves across various day types (Fig. S4.1 in Supplementary Materials 4) demonstrate the amount of energy bats can save by spending a full day torpid during colder conditions, although the lack of foraging means that their reserves will keep depleting until a warmer day arrives. The average decline in individual energy reserves on 'very warm' days from timestep 1 to the timestep before sunset ($t = 57$ for Nittedal and $t = 61$ for Trondheim) was 0.76g ± 0.06g in Nittedal and 0.56g ± 0.06g in Trondheim. On 'very cold' days in Trondheim and 'stable cold' days in Nittedal ('very cold' days were never recorded in July at this location) the bats lost respectively 0.03g and 0.04g (with little to no variation) of their energy reserves between the same two timesteps, thus using a mere 5.7% and 5.3% of these reserves on the warmer days.

Effects of environmental conditions and individual state

The combination of effects of photoperiod and state-dependency on the optimal diurnal routines for bats revealed strong responses in terms of the adaptive use of day-time torpor across day types (Fig. 3). On warm day types the percentage day-time torpor use decreased with increasing energy reserves (at the beginning of the day, $t = 1$) and with warmer weather conditions. On colder day types and in response to lower energy reserves on 'stable warm' days, bats expressed 100% torpor during day-time at each of the two locations. Photoperiod affected the day-time torpor expression on the warmer day types except for on 'very warm' days, with bats facing the lighter conditions of the Trondheim scenario generally expressing more torpor than conspecifics facing the darker Nittedal photoperiod, although the effect of energy reserves on torpor use were similar between locations (Fig. 3).

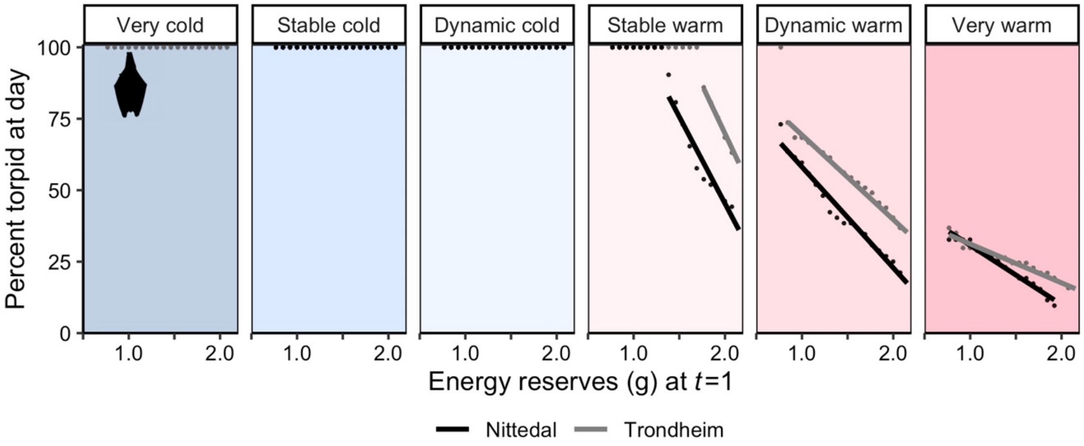


Figure 3: Model results for the percentage of expressed activity in 'torpor' in relation to individual fat reserves at the first timestep of the day (x-axis), temperature conditions (vertical panels left to right) and light photoperiod scenarios (dots per model run with best-fit lines for Nittedal in black and Trondheim in grey). Results are shown as separate dots for 100 one-day model runs for each location and fat reserve level scenario (only including fat reserves between the natural range of the initial simulation outputs, being 0.8 to 2.5g). Only percent of torpor expression is shown in this figure as the bats otherwise only rested during day-time. There are no datapoints from the Nittedal bat population on 'very cold' days because this day type had an occurrence probability = 0 for this scenario.

The optimal night-time decision to use torpor, resting or to forage was more complex in response to individual state and environmental conditions. Increasing individual energy reserves before sunset (i.e. at $t = 58$ for the Trondheim scenario, and $t = 55$ for the Nittedal scenario) had a generally negative effect on nightly foraging across all day types and locations (Fig. 4, top row), except for the two coldest day types on which all bats spent the whole night torpid. On 'dynamic cold' days, all bats used torpor at some point at night when they were not out foraging (Fig. 4, middle row), and individuals with greater energy reserves before sunset spent less time foraging and more time torpid than individuals with lower levels of energy reserves. For this day type, there was also no apparent effect of photoperiod (i.e. the Nittedal versus Trondheim scenarios) on either foraging or torpor (Fig. 4).

Nightly foraging was not markedly different across light- and weather conditions on the warmer day types, although bats in Trondheim spent slightly more of the night foraging than conspecifics in Nittedal (Fig. 4, top row), while torpor use (Fig. 4, middle row) and resting (Fig. 4, bottom row) varied with both environmental conditions and location. The state-dependent effect of nightly torpor use changed direction from positive to negative with increasingly warmer day types in combination with higher energy reserves, but this shift happened at higher energy reserves and during warmer conditions for the Trondheim scenario than for the darker Nittedal scenario (Fig. 4, middle row). This shift was caused by the gradual increase in time spent resting at night (Fig. 4, bottom row), because individuals would decrease foraging time with increasing energy reserves, but at higher temperatures and energy reserves bats would exchange the remaining time spent torpid with time spent resting in the roost instead. However, while heavier bats facing the darker Nittedal light conditions would exchange all their torpor use for time resting, this was only the case for the very heavy bats during warmer day types when experiencing the lighter night-time conditions of Trondheim, except during nights of 'very warm' days. For 'very warm' day types, the effect of the photoperiod on the three different activities was more similar, indicating that at very high or very low temperatures the photoperiod is less important for nightly behavioural responses than at intermediate temperatures.

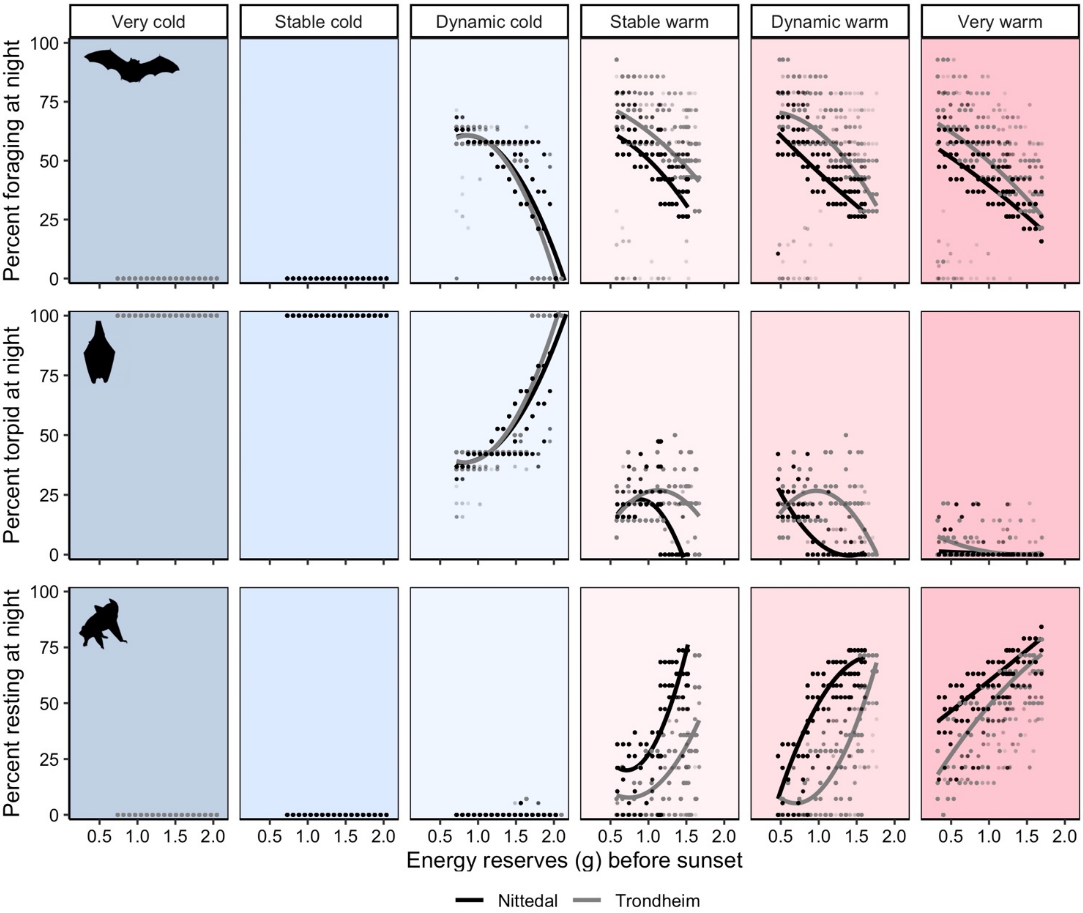


Figure 4: Model results for the percentage of expressed activity in 'foraging' (top panels), 'torpor' (middle panels) and 'resting' (lower panels) during night-time in relation to individual fat reserves before sunset (x-axes), temperature conditions (vertical panels left to right) and light photoperiod scenarios (dots per model run with best-fit polynomial lines for Nittedal in black and Trondheim in grey). Results are shown as separate dots for 100 one-day model runs for each location and fat reserve level scenario (only including fat reserves between the natural range of the initial simulation outputs for timestep 1, being 0.8 to 2.1g). Different fat reserves were implemented at timestep 1 and decreased across the day, depending on individual torpor vs. resting activities before night-fall. The large scattering of datapoints is due to implemented stochasticity in foraging success per timestep, affecting the continuous fat levels and thus the optimal decisions. There are no datapoints from the Nittedal bat population on 'very cold' days because this day type had an occurrence probability = 0 for this scenario.

Comparison of model predictions with empirical data

Overall, there was very good correspondence between our field data and the model predictions when using only the *a priori* parameter values from the literature and our own studies (Table 1a and Table 1b), plus the already established non *a priori* parameter values from the base model (Supplementary Materials 3). To provide more realistic quantitative comparisons, we matched sample sizes by using only the same number of model runs as we have samples from the field, considering the sample size for each day type in the model as in the empirical data.

Day-time torpor expression

Comparing the empirical data and model simulations of day-time torpor use at each location revealed strong similarities between observations and model results (Table S5.1 and Fig. S5.1 in Supplementary Materials 5). We performed Welch two sample t-tests between the field data and the model data for each location but found no significant difference between the means (for Nittedal: p-value = 0.86; for Trondheim: p-value = 0.38). However, although the sample sizes of bats at each day type at each location is similar between simulated model runs and empirical data, temperature cycles within day types still vary in the field data while it does not vary within day types in the model scenarios. Both the empirical data and the model simulation results revealed negative effects of increasing mean day-time air temperatures on day-time torpor expression (Fig. S5.1b), and although this effect was similar between the empirical data and model simulations for the Trondheim scenario, the model scenario for the Nittedal population showed an apparently stronger negative effect of the mean temperature than what was recorded in the empirical data. However, whether this is caused by discrepancies between the model and the field conditions, or if it is coincidental due to a small sample size at this particular location (N_{day} = 7), is not possible to determine here.

Night-time foraging, torpor and resting

For the nightly time allocation on foraging, torpor use and resting, the model simulations were again very similar to the empirical field data at the Trondheim location (Table S5.1 and Fig. 5a-c), revealing no significant differences between the means when tested with Welch two sample t-tests (foraging: p-value = 0.67; torpor use: p-value = 0.59; resting: p-value = 0.46). Larger differences were seen between the empirical data and the model simulations at the Nittedal location (Table S5.1 and Fig. 5a-c), although the means for torpor use and resting were not significantly different (torpor use: p-value = 0.78; resting: p-value = 0.11), while the means for time spent foraging revealed significantly more time spent on foraging in the empirical data than in the model simulations (p-value < 0.05). The temperature effect on the nightly behaviour showed positive impacts on the foraging and resting decisions and negative effects on the nightly torpor use; however, all these effects were apparently stronger in the model simulations than in the empirical data for the Nittedal scenario (Fig. 5d-f), which again is not possible to determine the causation of due to lack of field data from this location.

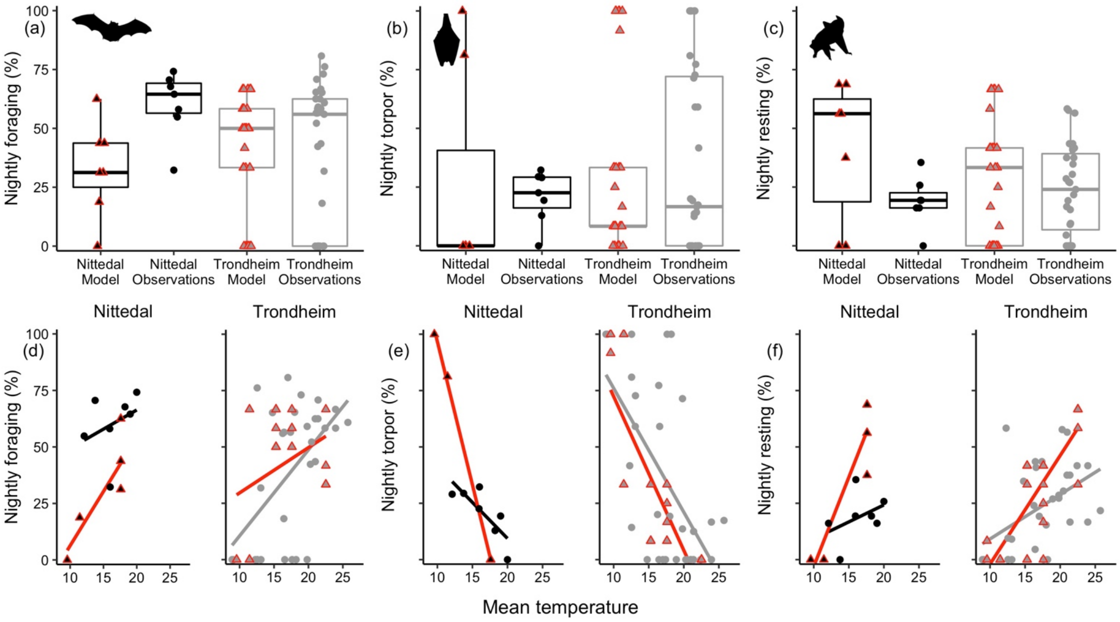


Figure 5: Comparisons of night-time ‘foraging’ (%), ‘torpor use’ (%) and ‘resting’ (%) from field derived data (round points) and from model simulations (triangle points with red outline) for the two locations of Nittedal (black points and boxes) and Trondheim (grey points and boxes). **(a)** Boxplots of nightly foraging between locations and data origin with boxes marking the data median and the 25th and 75th percentiles. **(b)** Boxplots of nightly torpor use between locations and data origin. **(c)** Boxplots of nightly resting between locations and data origin. **(d)** Positive effects of increasing mean daily temperatures on nightly foraging, both in the empirical data (round points and black or grey lines) and in data generated from matched simulated model runs (triangle points and red lines) for the two locations. **€** Negative effects of increasing mean daily temperatures on nightly torpor expression, both in the empirical data and in data generated from matched simulated model runs for the two locations. **(f)** Positive effects of increasing mean daily temperatures on nightly resting, both in the empirical data and in data generated from matched simulated model runs for the two locations.

Comparing model predictions across a latitudinal gradient

By first running ‘backwards’ calculations of optimal decisions followed by ‘forward’ simulating 200 individuals across one summer month at five different latitudes (see Fig. 6), we were able to reveal location-specific differences in both diurnal routines and optimal levels of each behaviour, as well as in survival probabilities. We explored potential limitations to location-specific survival by increasing and decreasing the intercept for daily temperature cycles by 2°C, simplifying scenarios for potential climate change effects at each location. These results are shown in panels in Figure 6 with the survival probability across 30 days from the baseline scenario for each location shown in the middle row of each set of panels. The results indicate that our simulated populations from Nittedal up to Tromsø were buffered against changes in temperatures by adjustments in their behavioural routines, although model bats in Tromsø showed signs of being at the very limit of their distributional range, with only slight effects on the summer survival if the mean temperature increased or decreased. Model bats in Gamvik were well beyond the distribution limit for survival given our model parameterization, and none of the temperature scenarios allowed them to survive past the 30 modelled days.

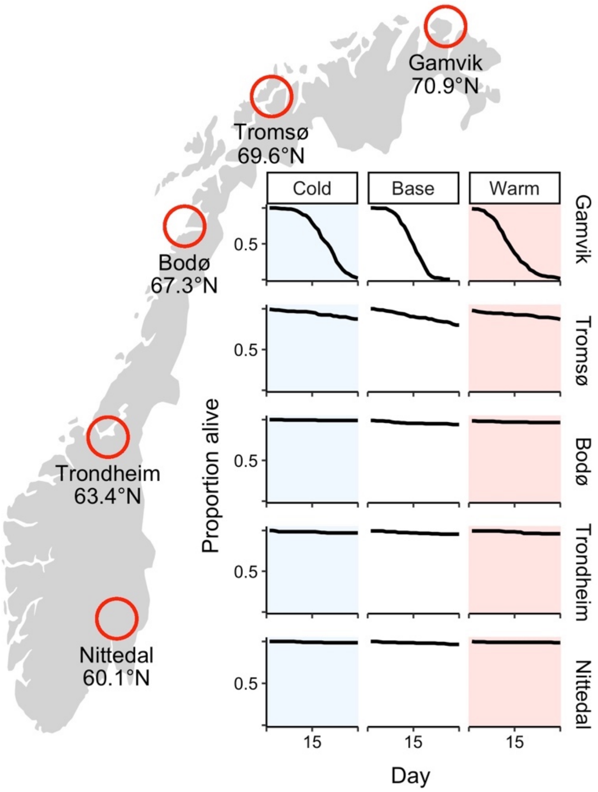


Figure 6: Survival probabilities from forward simulations of 200 individuals across one summer month (30 days) at five locations across a latitudinal gradient in Norway for different intercepts of the diurnal temperature cycle. Middle panes (white background) show scenarios with baseline values for each location, left panes show survival scenarios given a 'cold' temperature scenario (blue background), while right panes show scenarios given a 'warm' temperature scenario (pink background). The 'cold' temperature scenario corresponds to a decrease in the baseline temperature intercept of 2°C, whilst the 'warm' temperature scenario corresponds to an increase of 2°C.

When summarizing all individual simulations across the time horizon for all day types, the model bats in Nittedal showed the highest levels of resting during day-time on warmer day-types (Fig. 7). Model bats showed decreasing levels of day-time resting behaviour and increasing levels of torpor expression with increasing latitude on the same day-types. Given that the temperature cycles within day-types were the same across latitudes, the differences in daily torpor-strategies in Figure 7 must mostly be the result of variation in summer light levels, and hence foraging possibilities and individual energy reserves.

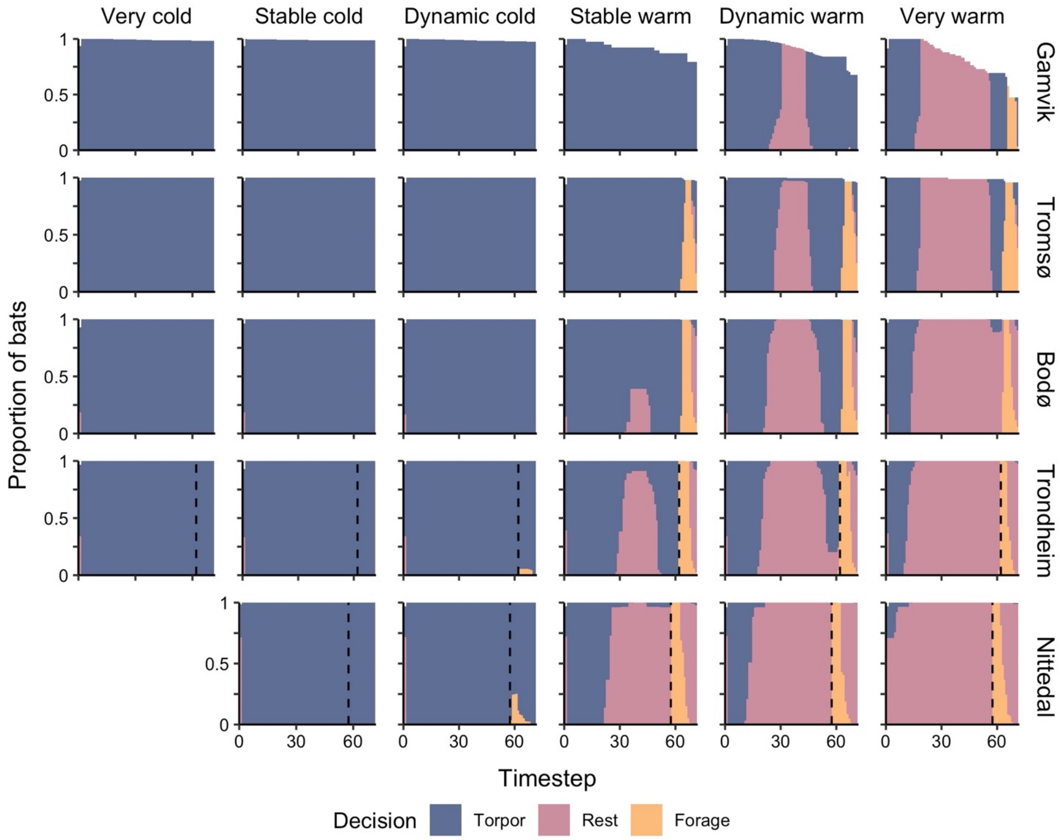


Figure 7: Summary plots across all day-types from forward simulations of 200 individuals at each of the five latitudes, illustrating the general behavioural patterns across the diurnal cycle at each location. Dark blue signifies when bats were expressing ‘torpor’, pink signifies ‘resting’, and yellow signifies ‘foraging’. Dashed vertical lines indicate sunset in Nittedal and Trondheim, while the sun in Bodø, Tromsø and Gamvik does not go down below the horizon during this summer month. ‘Very cold’ day types are not shown for the Nittedal location because such days were never recorded during July in Nittedal and thus had an occurrence probability of 0 in the model.

Diurnal fluctuations in energy reserves across warm day-types for each of the five locations showed that model bats in Nittedal spent more energy during day-time because they spent more time awake and resting, but they compensated for this mass loss by gaining markedly more foraging reserves at night than bats at any other location (Fig. S4.1 in Supplementary Materials 4). The average mass gain for foraging bats when comparing the body mass of timestep 57 to the maximum body mass of the following night on ‘very warm’ days was 1.1g ± 0.11 in Nittedal, 0.85g ± 0.15 in Trondheim, 0.81g ± 0.19 in Bodø, 0.84g ± 0.32 in Tromsø and 0.54g ± 0.17 in Gamvik. The greater foraging gain in Nittedal was due to the earlier sunset in the south of Norway, which allows bats to exit the roost to forage before the ambient temperature, and consequently the insect density, declines to its lowest levels due to lower overnight temperatures. Lighter nights further north also led the model bats at higher latitudes to stop their mass gain at lower levels as the predation risk increased with mass. Therefore, the bats in Nittedal were able to spend more time awake during the day, as they often had the chance to fully replenish their reserves during the following night. In contrast, model bats in Tromsø spent the whole day-time on even 'stable warm' days in torpor (Fig. 7), and thus lost less day-time body mass than the bats further south, but this was mostly because their foraging prospects were less good with limited time to forage and fewer insects available. For the northernmost location in Gamvik, most model bats did not forage until the occasional 'very warm' day, although no sequence of behaviours allowed them to survive throughout the whole summer month given the baseline parameterization values.

Discussion

Our study describes the state-dependent optimal behaviour of small bats facing environmental and physiological challenges of high-latitude living in summer. By exploring the diurnal routines in the use of three activities ('foraging', 'resting', and 'torpor'), we are able to show the various possible effects on individual behavioural strategies maximizing energy gain versus expenditure, and ultimately survival and limits to species northern geographical ranges. We can confirm that temperature cycles, and the strategic use of energy reserves, are important drivers of diurnal patterns in behavioural and physiological decision-making in bats, and specifically the strategic use of torpor. Such strong state-dependency is perhaps expected from the behavioural ecology literature (mostly on birds, Clark & Mangel 2000), but is not well explored in heterothermic endotherms and should contribute to our future understanding of strategic decisions in the order of Chiroptera.

A few empirical studies have demonstrated state-dependency regarding torpor expression in heterotherms, where animals with more energy reserves spent less time torpid, for example woodchucks (*Marmota monax*: Zervanos *et al.* 2014), dormice (*Glis glis:* Bieber *et al.* 2014), and bats *(Myotis myotis*: Wojciechowski *et al.* 2007; *Myotis lucifugus*: Matheson *et al.* 2010; *Plecotus auritus*: Sørås *et al.* 2022). Our model predictions of day-time torpor use are consistent with these findings, showing that individuals with lower energy reserves benefit to a greater extent from torpor energy savings, whilst individuals with greater energy reserves benefit from instead spending more time awake and resting. However, these responses are temperature dependent and vary most during night-time and the bats' active period. This suggests that both the environmental conditions and any strategic diurnal activity patterns need to be taken into account when testing for state-dependent effects on behavioural and physiological decision-making.

The implementation of realistic and dynamic time- and/or temperature-dependent parameters in our model framework should result in quantitative predictions that match the relative costs and benefits for foraging, torpor and resting in our natural bat populations. As hoped, comparisons of day-time and night-time behavioural decisions in our empirical data on northern bats versus data generated from the model simulations showed strong similarities. However, the model underestimated the proportion spent foraging at the lower latitude location (Nittedal) compared to the field observations (Table S5.1, Fig. 5), but due to a small sample size for this population we were unable to determine if this was caused by actual differences between field observations and model parameters or just by chance in the sampling. The data collected at the higher latitude location (Trondheim) involved a much larger sample size and showed greater levels of variation in behavioural decisions across mean daily temperatures (Fig. S5.1b and 5d-f), which was also reflected in the model results, presumably caused by (stochastic) variation in individual energy reserves. The model comparisons for this location matched very well with the field observations, indicating that our model incorporates important drivers for general strategies in the behaviour and physiology of a range of individual bats in the studied species.

The forward simulation patterns of daily torpor use across the full Norwegian latitudinal gradient showed that, except for on 'very warm' days in the Nittedal scenario, all model bats employed torpor during the morning. On any of the warm day types in Nittedal, or on 'very warm' days in Trondheim and Bodø, the bats would mostly rewarm early and stay awake and resting until the evening, whilst bats on ‘stable warm’ or ‘dynamic warm’ days in Trondheim and Bodø, or on ‘dynamic warm’ and ‘very warm’ days in Tromsø or Gamvik, would re-enter torpor again in the afternoon and only rewarm again around sunset to forage (see Fig. 7). This closely matches northern bat behaviour recorded during the summer in Nittedal and Trondheim, corresponding to the two most commonly observed patterns in daily torpor use across bat species and climate zones (Fjelldal *et al.* 2022). These patterns involve either the ‘one-bout’ pattern (one torpor bout expressed daily) or the ‘W-shaped’ pattern (two torpor bouts expressed, one in the morning and one in the afternoon). Our model confirms that a main driver of these patterns is likely the diurnal temperature cycles within the roost (Turbill *et al.* 2008; this study), as well as state-dependency and prospect of successful foraging (Wojciechowski *et al.* 2007; this study). Bats in Nittedal were able to leave the roost to forage earlier than populations further north, and therefore profited from longer nights and higher prey availabilities, and this allowed them to spend more time awake during the day as their energy reserves could be fully replenished at night. Bats at higher latitudes adjusted their energy expenditure according to their more limited foraging prospects, and thus expressed more torpor across the daily cycle the further north they were. These strategic behavioural and physiological decisions regarding energy saving and foraging acquisitions are therefore driven by complex interactions between both current and prospective environmental conditions and individual energetic state (Wojciechowski *et al.* 2007; Fjelldal *et al.* 2021; this study).

Field-studies investigating latitudinal effects on torpor expression in free-ranging heterotherms have already identified patterns of increased daily torpor use with increasing latitudes (Fenn *et al.* 2009; Stawski 2012b; Czenze *et al.* 2017). However, disentangling latitudinal effects from correlated temperature effects is challenging in field studies, although Czenze *et al.* (2017) found less torpor in a lower-latitude population of lesser short-tailed bats (*Mystacina tuberculata*) compared with higher-latitude living individuals across similar summer temperature conditions. This is in line with our model predictions, although Boyles *et al.* (2016) suggested that shifts in diet and foraging behaviour also could be used in response to environmental conditions at higher latitudes.

In our model framework, we only considered behaviours and trade-offs relevant for non-reproductive bats. Reproductive females face additional challenges during the summer as they go through highly energetically expensive periods of gestation and lactation while risking delays in the foetus development or reductions in milk production if they enter deep torpor to save energy (Racey & Swift 1981; Wilde *et al.* 1999). Pregnant and lactating bats therefore still use torpor, but only for short periods of time, and they maintain higher body temperatures in torpor than non-reproductive or post-lactating individuals (Dzal & Brigham 2013). A potential extension of our non-reproductive small-bat-in-summer model into one customised for reproductive female bats would thus also need to include not only the costs and benefits specifically related to reproduction and a modified measure of reproductive fitness plus survival, but also a multi-level body temperature state variable (e.g. see Brodin *et al.* 2017) and all of its consequences for foetal growth and survival, as opposed to our current ‘torpid’ versus ‘non-torpid’ two-level state variable. As our model does not include female reproduction, the results presented here regarding bat distributional ranges in Norway need to be interpreted as suitable environmental limits for general bat survival probabilities. Viable breeding colonies of bats have to navigate an even finer line between foraging, torpor and resting that encompasses the energetic requirements and costs of pregnancy and lactation (Kunz 1974; Kurta *et al.* 1989), and this will further affect any predictions of suitable environmental conditions for different species ranges across any latitudinal gradient.

Our non-reproductive model bat species is based upon quantified physiological estimates from several small-bodied bat species (see Supplementary Materials 1) and the distribution ranges predicted by our model correspond to the northernmost species in Norway, the northern bat. However, other bat species in Norway like the brown long-eared bat (*P. auritus*) or *Myotis spp*. are not found much further north than Trondheim (63.4°N). This suggests strong interspecific differences in distribution limits that require explanation. European insectivorous bat species show considerable interspecific variation in diet

(Rydell 1989; Vaughan 1997), foraging behaviour (Norberg & Rayner 1987; Jones & Rydell 1994) and light sensitivity (Rydell *et al.* 1996; Duvergé *et al.* 2000), which will affect any theoretical assumptions regarding the factors limiting the northern distributional ranges of different species. However, the inclusion of quantitative estimates concerning species-specific diets and energetic requirements is perhaps something that could be investigated through further development of our model. Our general framework of optimal decision making of small-bats-in-summer should therefore contribute to the understanding of behavioural adaptations to high-latitude living in the order of Chiroptera and offer opportunities for further explorations of species- or location-specific behavioural decision-making in bats during summer.

Conclusions

By developing a state-dependent stochastic dynamic programming model, we aimed to understand the strategic use of torpor in non-breeding bats facing the particular challenge of summer at high latitudes. Our simulations of general bat behaviour from our baseline model runs suggest that bats express the common adaptive diurnal routine in foraging and torpor versus resting observed in empirical studies as a response to particular combinations of temperature conditions, photoperiods (included as predation threat and energetic competition cost), individual energetic reserves and the anticipation of foraging profitability. Further simulating populations across a latitudinal gradient showed that the survival of bats inhabiting locations up to a certain latitude in Norway (≥ 67.3°N) was more or less buffered against environmental variation by such strategic use of torpor during the lightest summer month. Further north (69.6°N), the simulated bat populations seemed to be at the very edge of their distributional range limit as regards to summer survival, even with all their behavioural adjustments in torpor and foraging employed, which again aligns with the observed distributional range of northern bats in Norway.

Our model currently only considers the general survival challenges faced by non-reproductive small-bats-in-summer, but female reproductive bats face additional energetic challenges will affect the optimal use of torpor according to variation in environmental conditions. Distributional ranges of bats in Norway and elsewhere can only be properly investigated and understood by including the potential for breeding colony persistence, which should be possible via specific extensions of our model. As we demonstrate here, the powerful combination of state-dependent modelling and detailed empirical data collection can provide meaningful insight into environmental and physiological factors that drive behavioural decision-making of systems such as the small bat in summer, and a more complete understanding of the ecological limits of such species.

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Conflict of interest

We declare no conflict of interest.

Author contributions (CRediT roles)

Mari Aas Fjelldal: Conceptualization, Software, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing - original draft. **Amandine Sophie Muller**: Software, Data curation, Methodology, Writing- Reviewing and Editing. **Irja Ida Ratikainen**: Software, Data curation, Methodology, Writing- Reviewing and Editing. **Clare Stawski**: Conceptualization, Funding acquisition, Supervision, Writing- Reviewing and Editing. **Jonathan Wright**: Conceptualization, Investigation, Methodology, Supervision, Writing- Reviewing and Editing.

Data availability statement

R-codes for our model framework are included as r-scripts in the Supplementary Materials. The dataset used to compare model predictions and field observations are available from the corresponding author on reasonable request.

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Supplementary Materials 1: Parameterization details and justifications

We constructed a stochastic dynamic model with a parameterization as close as possible to values from natural study systems. Explanations and justifications for all of these parameterization values can be found below.

1.1. Quantified physiology

1.1.1 Cost of resting MR (C_{RMR}), basal MR (C_{BMR}) and torpor MR (C_{TMR})

For the temperature-dependent resting metabolic rate (RMR) and basal metabolic rate (BMR), we used data from the small-bodied (~7 grams) Australian bat species *Nyctophilus geoffroyi* published in a study by Geiser and Brigham (2000). No latitudinal nor climate zone effects have been found to affect metabolic rates in the order of Chiroptera after correcting for body size and temperature (Speakman & Thomas 2003; Cruz-Neto & Jones 2006; Skåra *et al.* 2021; Fjelldal *et al.* 2022), which should result in these metabolic rates being representative for small bats. Furthermore, the thermoregulatory curve (Fig. 3b in Geiser and Brigham (2000)) and BMR (1.36 ± 0.17 mL O_2 g^{-1} h^{-1}) of *N. geoffroyi* closely resembles what we find in the northern bats (*unpublished data*), which is the focal species in our empirical data comparisons (see main text).

Equation S1.1 (from Geiser and Brigham (2000)) estimates the mass specific oxygen consumption (mL O_2 g^{-1} h^{-1}) for temperatures below the lower critical temperature (T_{LC}) of 29.0 degrees:

$$\mathbf{C_{RMR}}: \quad \text{mL } O_2 \text{ g}^{-1} \text{ h}^{-1} = 11.69 - 0.35 \times \text{air temperature} \quad . \qquad \text{(S1.1)}$$

Temperatures above the T_{LC} belong to the species' thermal neutral zone (TNZ; °C > 29°C) with a temperature-independent BMR as described in equation S1.2 (below). Given the high latitude and generally mild summers found at the study locations, we assume that the roosts in our model are not heating up to temperatures that lead to further increases in the MR, the highest modelled roost temperature being 35.4° (see section 1.2.2).

$$\mathbf{C_{BMR}}: \quad 1.36 \pm 0.17 \text{ mL } O_2 \text{ g}^{-1} \text{ h}^{-1} \quad . \qquad \text{(S1.2)}$$

For the torpor metabolic rate (TMR), we implemented the equation derived from measuring torpid Norwegian brown long-eared bats, presented in Fjelldal *et al.* (2022). We chose not to use the TMR curve presented in Geiser and Brigham (2000), because it lacked TMR values > 0.4 mL O_2 g^{-1} h^{-1}, which meant that there was a large range between the highest measured TMR and the BMR that was unaccounted for. The TMR of Norwegian brown long-eared bats showed a similar curve to that of the Australian eastern long-eared bat *Nyctophilus bifax* (Fjelldal *et al.* 2022), and could constitute a general representation for TMR in small bats. The TMR was found to increase exponentially with body temperature (T_b), following equation S1.3 (Fig. 1 in Fjelldal *et al.* (2022)). However, small bats have been found capable of saving large amounts of energy through torpor expressions even at high temperatures (Reher & Dausmann 2021), and may stay torpid far into their TNZ (Sørås *et al.* 2022). Therefore, to avoid the exponential TMR curve increasing to unrealistically high values at high temperatures, we added a condition that TMR never increases above a value of $C_{BMR} \times 0.9$. This meant that a bat would always have the choice of saving energy by expressing torpor even at high temperatures:

$$\mathbf{C_{TMR}}: \qquad \text{mL O}_2\ \text{g}^{-1}\ \text{h}^{-1} = \begin{array}{ll} 0.0198 \times 1.137^{Tb} & \text{if } C_{TMR} < C_{BMR} \times 0.9; \\ C_{BMR} \times 0.9 & \text{if } C_{TMR} \geq C_{BMR} \times 0.9 \end{array} \quad . \qquad (S1.3)$$

Using the values from Geiser and Brigham (2000) and Fjelldal *et al.* (2022), we estimated energy consumption and eventually the weight loss at different temperatures (see section 1.1.4 below for converting the MR into weight loss).

1.1.2 Rewarming cost (C_{RW})

Heterotherms may save large amounts of energy by employing torpor, but face a temperature-dependent cost of active rewarming when choosing to exit this state (Turbill *et al.* 2008; Currie *et al.* 2015). The total cost of active arousals was quantified in *N. geoffroyi* at different environmental temperatures by Turbill *et al.* (2008), and described with the following equation:

$$\mathbf{C_{RW}}: \qquad \text{kJ} = 0.84 - 0.026 \times \text{air temperature} \quad . \qquad (S1.4)$$

A second equation was presented in the original study where the net passive rewarming energy expenditure was included (see Fig. 5 in Turbill *et al.* (2008)); however, as each timestep in our model consists of a temperature-dependent TMR value this is already accounted for. We therefore chose to implement equation S1.4 as the quantified cost of arousal in our model, after converting it into weight loss (see section 1.1.4 below).

1.1.3 Flight cost (C_{flight})

The energetic cost of flying was calculated for free-ranging little brown bats (*Myotis lucifugus*) by Kurta *et al.* (1989). The study calculated that the cost of foraging flight of a 9 g *M. lucifugus* was 4.46 kJ h^{-1}, a value which we implemented in our model. Another option would be to rearrange the equation provided by Thomas (1975) to estimate energy consumption during flight; however, this equation should be used with caution, particularly for species with small body masses (Kunz 1980). In the study by Kurta *et al.* (1989), the calculated flight requirements for female brown bats were 13% lower than what Thomas' equation predicted. As the northern bats are approximately the same in size as the little brown bats, we used the calculation of their flight energy requirements in our model after converting the value into weight loss (see section 1.1.4 below).

1.1.4 Converting physiological measurements into weight loss (g)

As our model represents unreproductive bats during summer, we assume that the main source of daily weight fluctuations is caused by stomach contents rather than by changes in fat reserves. According to the diet composition and conversion factors described in Kurta *et al.* (1989), one gram of fresh insects corresponds to 7.25 kJ of ingested energy, 6.12 kJ of assimilated energy, or 5.51 kJ of metabolized energy. We chose to use the estimates of ingested energy, where the energy density (7.25 kJ g^{-1} wet mass) resemble the results found when performing a bomb calorimetry (Kunz 1988). Knowing this, we converted the values obtained from respiratory studies into kJ and further into grams.

First, oxygen consumption was converted into CO_2 production: a typical insect diet consists of 70% water, 17.8 % protein, 4.6 % fat and 2.2 % carbohydrates (Kurta *et al.* 1989). Disregarding the water content, the diet consists of 72.4 % protein, 18.7 % fat and 8.9 % carbohydrates. In order to convert O_2 consumption to CO_2 production, the nutrient mixture in the diet should be considered due to its effect on the metabolism. We considered the following respiratory exchange ratios (RER = VCO_2 /

VO_2) for the different components: 0.82 for protein; 0.70 for fat; and 1 for carbohydrates. Applying this to the mixed typical insect diet, we arrived at a RER = (0.82 × 0.724) + (0.70 × 0.187) + (1 × 0.089) = 0.81358. We then utilized this RER value in order to estimate VCO_2 produced from VO_2 consumed.

Second, after estimating VCO_2, the VCO_2 was further converted into kJ. Each liter of CO_2 produced represents 27.2 kJ of assimilated energy (Kurta *et al.* 1989), and the estimates of VCO_2 were therefore first converted from mL to L and then further into kJ.

Finally, the estimated kJ was converted into loss of grams based on a conversion factor of 7.25 kJ = 1 gram wet mass (Kurta *et al.* 1989). The cost of RMR, BMR, TMR and the flight cost were calculated as hourly weight losses and was further converted into a cost per timestep in the model, while the cost of rewarming was kept as an overall total weight loss. Table S1.1 shows the conversion of each of the values from the original measurement to the estimated weight loss in grams.

Table S1.1: The step-wise conversion of each of the physiological measurements into weight loss in grams. Note that the units are different for C_{RW} and C_{flight} than what is described in the column header.

Parameter	mL O_2 g_{bat}^{-1} h^{-1}	mL CO_2 g_{bat}^{-1} h^{-1}	kJ g_{bat}^{-1} h^{-1}	g (g_{bat}^{-1} h^{-1})
C_{RMR}	$11.69 - 0.35 \times T_a$	$9.51 - 0.285 \times T_a$	$0.259 - 0.0078 \times T_a$	$0.0357 - 0.0011 \times T_a$
C_{BMR}	1.36	1.106	0.0301	0.0042
C_{TMR}	0.0198×1.137^{Tb}	$0.0161^{0.1284 \times Tb}$	$0.0004^{0.1284 \times Tb}$	$0.00006^{0.1284 \times Tb}$
C_{RW}			$0.84 - 0.026 \times T_a$ (kJ)	0.11586 – 0.003586 (g)
C_{flight}			4.46 (kJ h^{-1})	0.615 (g h^{-1})

1.2. Quantified environmental conditions

1.2.1 Air temperature cycles across different day-type scenarios

In our model framework, we implemented dynamic time-dependent temperature cycles, modelling realistic environmental conditions bats may face across days and nights. We were interested in six general day types to catch variability in mean temperatures and daily temperature fluctuations alike: 'very warm' days; 'dynamic warm' days; 'stable warm' days; 'dynamic cold' days; 'stable cold' days; and 'very cold' days. To quantify the daily temperature cycles and the probability of each day type, we downloaded temperature data recorded every 10 minutes (if available, otherwise 1-hour recordings were used) from the Norwegian Centre for Climate Services webpage for the month of July across 9-10 years at each of the five locations (see table S1.2 for details). Not all stations or locations had temperature data recorded for July each year, which is why stations vary within location and years vary between locations.

We categorized each day (defining one day as the time between sunrise to the following sunrise) as one of six day types based on the following criteria:

1. 'Very warm' day: mean daily temperatures > 20°C and daily maximum temperatures > 26°C;
2. 'Dynamic warm' day: mean daily temperatures > 14°C and daily temperature ranges ≥ 6°C;
3. 'Stable warm' day: mean daily temperatures > 14°C and daily temperature ranges < 6°C;
4. 'Dynamic cold' day: mean daily temperatures ≤ 14°C and daily temperature ranges ≥ 3°C;
5. 'Stable cold' day: mean daily temperatures ≤ 14°C and daily temperature ranges < 3°C;
6. 'Very cold' day: mean daily temperatures < 9°C, minimum daily temperature < 6°C and maximum daily temperature < 13°C.

We converted the time of day into 72 timesteps between sunrise and the following sunset, corresponding to 20 minutes per timestep (following the timeframe used in our model framework – see main text), and fitted sixth order polynomial models for each day type to quantify the daily temperature cycles (Fig. S1.1). The polynomial models were fitted based on data from all five locations. We finally calculated the occurrence probability of each day type at each location based on the number of days in each category in relation to the total number of days (Fig. S1.2). The probabilities for each day type were accounted for when computing the optimal decisions in the backwards iterations by calculating the expected energy reserves and fitness values for each day type at timestep 1 for the next day, if the current timestep was the last timestep of the current day ($t = 72$). A weighted mean (based on the day type occurrence probabilities) for the expected fitness values for each decision was then calculated across day types for each energy reserve state level. In the forward simulation, the day types were included as stochastic variables by drawing day type sequences based on the occurrence probabilities.

Table S1.2: Details regarding the temperature data obtained for the month of July from the Norwegian Centre for Climate Services webpage.

Location	Year	Station	Data measurement intervals
Nittedal			
	2012	SN18280	10 minutes
	2013	SN4460	1 hour
	2014	SN18280	10 minutes
	2016	SN18280	10 minutes
	2017	SN18280	10 minutes
	2018	SN18280	10 minutes
	2019	SN18280	10 minutes
	2020	SN18280	10 minutes
	2021	SN18280	10 minutes
Trondheim			
	2012	SN68860	1 hour
	2013	SN68860	1 hour
	2014	SN68175	10 minutes
	2015	SN68860	1 hour
	2016	SN68175	10 minutes
	2017	SN69035	10 minutes
	2018	SN68175	10 minutes
	2019	SN68175	10 minutes
	2020	SN68175	10 minutes
	2021	SN68175	10 minutes
Bodø			
	2011	SN82290	10 minutes
	2012	SN82290	10 minutes
	2013	SN82290	10 minutes
	2014	SN82290	1 hour
	2015	SN82290	10 minutes
	2016	SN82220	10 minutes
	2017	SN82220	10 minutes
	2018	SN82220	10 minutes
	2019	SN82220	10 minutes
	2020	SN82220	10 minutes
Tromsø			
	2011	SN90490	1 hour
	2012	SN90490	1 hour
	2013	SN90490	1 hour
	2014	SN90490	1 hour
	2015	SN90490	1 hour
	2016	SN90490	1 hour
	2017	SN91180	10 minutes
	2018	SN91180	10 minutes
	2019	SN91180	10 minutes
	2020	SN91180	10 minutes
Gamvik			
	2012	SN96310	1 hour
	2013	SN96310	1 hour
	2014	SN96310	1 hour
	2015	SN96310	1 hour
	2016	SN96310	1 hour
	2017	SN98265	10 minutes
	2018	SN98265	10 minutes
	2019	SN96310	1 hour
	2020	SN98265	10 minutes
	2021	SN96310	1 hour

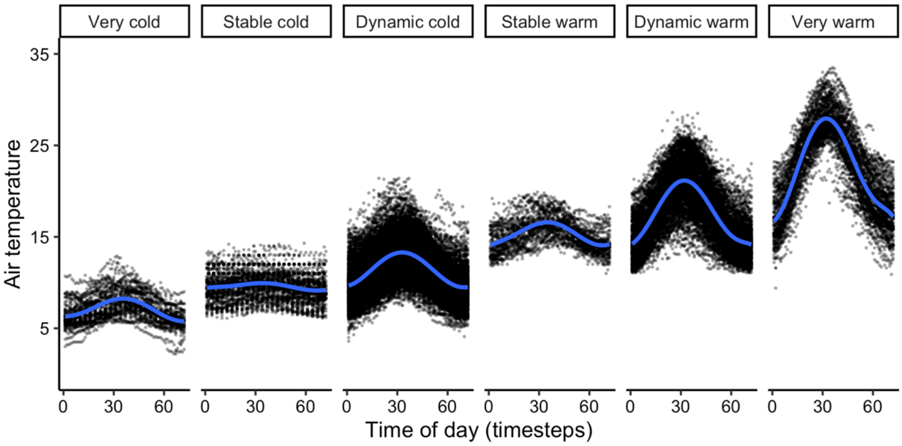

Figure S1.1: Daily temperature cycles for each day-type from sunrise (timestep = 1) to the last timestep before the following sunrise (timestep = 72). Black dots are the recorded temperatures across locations and years during the full month of July, while blue lines show fitted six-degree polynomial models for each day-type.

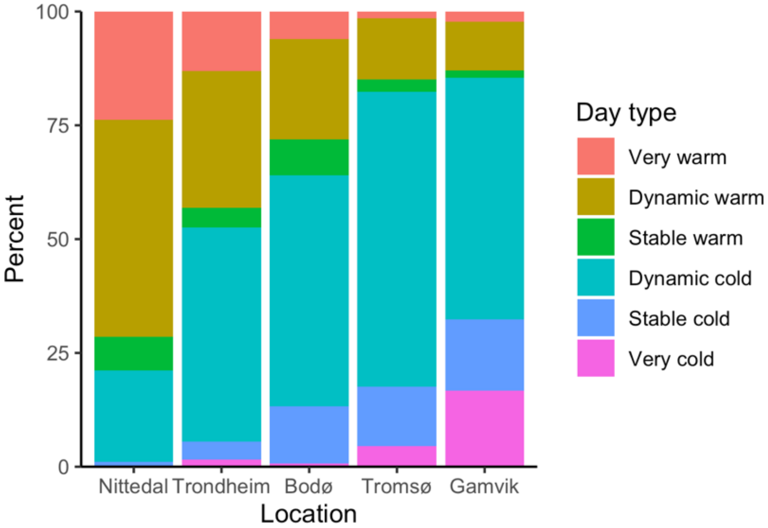

Figure S1.2: Occurrence probabilities of each day-type during July across locations. The exact probabilities for, respectively, ‘very warm’ days, ‘dynamic warm’ days, ‘stable warm’ days, ‘dynamic cold’ days, ‘stable cold’ days and ‘very cold’ days at each location were: 0.0, 0.01, 0.20, 0.07, 0.48 and 0.24 in Nittedal; 0.02, 0.04, 0.47, 0.04, 0.30 and 0.13 in Trondheim; 0.01, 0.12, 0.51, 0.08, 0.22 and 0.06 in Bodø; 0.04, 0.13, 0.65, 0.03, 0.13 and 0.02 in Tromsø; 0.17, 0.16, 0.53, 0.01, 0.11 and 0.02 in Gamvik.

Equations S1.5 to S1.10 below describes the sixth-degree polynomial model equations for the temporal (dependent on timestep (*t*)) air temperature cycles for each day type:

‘Very warm’ days: $16.58^{\circ}C + 0.12 \times t + 0.024 \times t^2 - 8.99 \times 10^{-5} \times t^3 - 2.95 \times 10^{-5} \times t^4 + 6.01 \times 10^{-7} \times t^5 - 3.38 \times 10^{-9} \times t^6$ (S1.5)

‘Dynamic warm’ days: $14.11^{\circ}C + 0.11 \times t + 0.009 \times t^2 + 2.53 \times 10^{-4} \times t^3 - 2.56 \times 10^{-5} \times t^4 + 4.47 \times 10^{-7} \times t^5 - 2.36 \times 10^{-9} \times t^6$ (S1.6)

‘Stable warm’ days: $13.95^{\circ}C + 0.11 \times t - 0.007 \times t^2 + 5.62 \times 10^{-4} \times t^3 - 1.82 \times 10^{-5} \times t^4 + 2.30 \times 10^{-7} \times t^5 - 1.00 \times 10^{-9} \times t^6$ (S1.7)

‘Dynamic cold’ days: $9.62^{\circ}C + 0.04 \times t + 0.008 \times t^2 - 8.43 \times 10^{-5} \times t^3 - 6.03 \times 10^{-6} \times t^4 + 1.24 \times 10^{-7} \times t^5 - 6.43 \times 10^{-10} \times t^6$ (S1.8)

‘Stable cold’ days: $9.39^{\circ}C + 0.03 \times t - 0.004 \times t^2 + 2.89 \times 10^{-4} \times t^3 - 8.41 \times 10^{-6} \times t^4 + 1.03 \times 10^{-7} \times t^5 - 4.43 \times 10^{-10} \times t^6$ (S1.9)

‘Very cold’ days: $6.31^{\circ}C + 0.005 \times t + 0.002 \times t^2 + 1.80 \times 10^{-4} \times t^3 - 9.02 \times 10^{-6} \times t^4 + 1.27 \times 10^{-7} \times t^5 - 5.68 \times 10^{-10} \times t^6$ (S1.10)

1.2.2 Roost temperature cycles across different day-type scenarios

Roost temperatures can be markedly different from outside air temperatures, depending on roost characteristics (e.g. Kerth *et al.* 2001; Lausen & Barclay 2003; Lourenço & Palmeirim 2004; Stawski *et al.* 2008; Michaelsen *et al.* 2014). Our model framework incorporates temperature-dependent physiological energetics (i.e. metabolic rates and rewarming costs), and given our assumptions that bats could only employ torpor or the resting behaviour while inside their respective roosts we attempted to implement realistic roost temperature cycles that depended on, but that were not necessarily identical to the outside air temperature. For this model framework, we used our own estimates of roost temperature, as described below.

All our radio-tagged northern bats from the field (see details in the main text Methods section) roosted under the roofs of houses or sheds during our data collection period. Upon losing their transmitters, three of these were dropped while the bats were still in their roosts and kept on recording temperature data for a prolonged period of time, logging the roost temperature. Although we could not verify the exact location of the tags within the roosts, we assumed they were reasonably close to where the bats had been roosting, and thus recorded temperature conditions representing the environment experienced within the roost. The daily temperatures recorded in the roosts showed large fluctuations on most days, with the total temperature range recorded being 9.6°C to 42.1°C (Fig. S1.3).

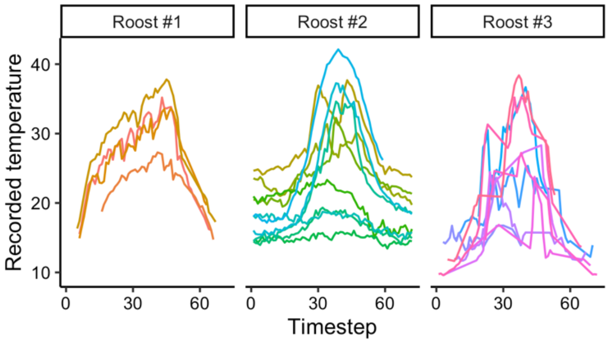

Figure S1.3: Recorded roost temperature across the daily cycle (between sunrise and the following sunrise, one timestep corresponding to 20 minutes) for three different roosts, all located under the roofs in houses. Each coloured line represents measurements across one day.

A total of 23 days of roost temperature data were recorded across the three transmitters lost in the roosts. Simultaneous outside air temperature data were recorded every 10 minutes using small heat-sensitive data loggers (0.5°C, DS 1921G Thermochron iButtons, Maxim Integrated Products, Inc., Sunnyvale, CA, USA) placed inside cardboard cups and hung from tree branches ~1.5 meters above the ground outside of each roost. By subtracting the measured air temperature from the roost temperature, we obtained a measure of the difference between air temperature and roost temperature across the 23 days of data.

Based on the outside air temperature, we defined each day as one out of six day types (as explained in section 1.2.1 above). Because we did not have enough data to determine the different roost temperature trajectories for all six day types, we made a simplified assumption of categorizing 'cold' day types ('very cold', 'stable cold' and 'dynamic cold') and 'warm' day types ('very warm', 'stable warm' and 'dynamic warm'), resulting in 6 days in the 'cold days' category and 17 days in the 'warm days' category. The daily trajectories of temperature differences between roost temperature and air temperature are shown in figure S1.4, illustrating how the roosts warmed up markedly more than the outside air temperature on 'warm' days (likely due to the sun warming up the roofs under which the bats were roosting), while on 'cold' days the roosts had a slightly higher but stable temperature compared to the outside air temperature. For simplicity (and due to the low sample size for 'cold' days) we defined roost temperature on any of the 'cold' day types as a constant 2 degrees higher than the outside air temperature in our model, while the roost temperature on 'warm' day types were defined with a 3rd degree polynomial model (as shown in Fig. S1.4; equation specified in Table 1a in Methods).

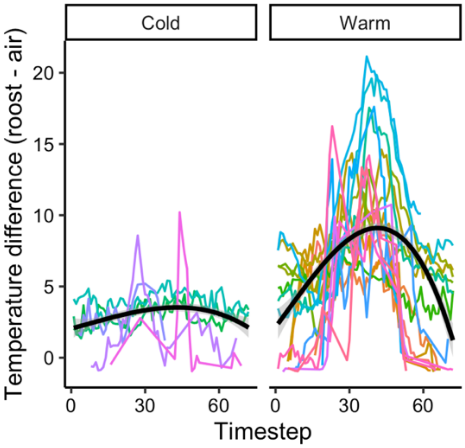

Figure S1.4: Temperature differences between the recorded roost temperature and the outside air temperature across the daily cycle (between sunrise and the following sunrise, one timestep corresponding to 20 minutes) for 'cold' and 'warm' day types. Black lines show fitted three-degree polynomial models for each day-type category.

1.2.3 Food availability

For our study system, we used insectivorous bats as model organisms. About 70% of all bat species feed on insects (Jones & Rydell 2005), a food source that is heavily affected by seasonal and environmental fluctuations, and particularly air temperature (Anthony & Kunz 1977; Speakman *et al.* 2000; Stawski 2012a). For our model, we considered the findings by Speakman *et al.* (2000) where variation in bat activity and prey abundance were correlated with air temperature, linking the insect abundance to daily temperature cycles (see Fig. 2 in Speakman *et al.* (2000)). Using this figure as our reference point, we created the following equation (S1.11) regarding temperature-dependent insect abundance:

Food abundance (proportion): $1 / (1 + \exp(-0.524 \times (T_a - 8))$ (S1.11)

This equation produces a logistic curve for the temperature-dependent proportion of insect abundance (from 0-1; see Fig. 1c in the main text Methods). For our model, we further needed to include a net foraging intake to provide the energetic value the bats could obtain at each time-step when foraging. In the study by Sørås *et al.* (2022), brown long-eared bats were found to increase their body mass at capture with 0.009 grams per minute after sunset, indicating increased gut fill with increased foraging time. Converting this into an hourly value resulted in an expected increase in body mass of 0.54 g h^{-1}. For the purpose of our model, we were interested in including a net foraging intake, which meant accounting for flight costs and potential temperature effects on the foraging success. We therefore added the presumed C_{flight} of 0.615 g h^{-1} to the hourly body mass increase and, after calculating the mean nightly T_a for the capture nights at the study location (*unpublished data*), used the overall average nightly temperature (12.18°C) to account for expected food abundance using equation S1.11. With an estimated food abundance of 0.9 at 12.18°C, we arrived at a net foraging intake of ~1.3 g h^{-1}. The potential energy gain (α in the model) was tested in early models with three different values (1 g, 1.3 g, 1.6 g) to explore model sensitivity and how slightly higher and lower values altered the decision-pattern of bats in summer, and this verified that the calculated baseline value of 1.3 g h^{-1} generated realistic scenarios.

1.2.4 Light-dependent predation threat

Predation threat represents one of the main explanations for why bats are nocturnal creatures, although bat-catches by vertebrate predators seem to be mainly opportunistic (Lima & O'Keefe 2013). Nevertheless, the risk of being preyed upon by avian raptors has been estimated to be 100 to 1000 times higher during daylight compared with nocturnal hours (Speakman 1991a; Speakman 1991b; Speakman 1995). We therefore assumed a light-dependent predation threat, using our own collected light measurements (Fig. S1.5a) to estimate predation threats (Fig. S1.5b) across the daily cycle in Nittedal and Trondheim. Light conditions were measured in lux using an illuminance UV recorder (TR-74Ui data logger). These light recordings were then log-scaled (due to the massive range in measured lux), before they were converted to fit as a realistic predation risk ranging between 0 and up towards 1. The equation below (S1.12) shows the conversion from measured lux to an estimated predation risk:

$$\text{Predation threat:} \qquad = \frac{(\log(\text{lux}))^3}{270} \quad . \qquad \text{(S1.12)}$$

We fitted fifth order polynomial models to represent the fluctuations in light-dependent predation threats throughout the day, but specified a minimum threshold-value of 0.0001 as some of the estimated values from the fitted models were negative during night-time, and an upper threshold-value of 0.2 because of assumptions that the predation threat would be light-independent above certain light-levels. For simplicity, the estimated predation threat in the model did not differentiate between the six different day types.

As we did not have light-measurements from higher latitudes than Trondheim, we downloaded sun altitude data per 20 minutes for July at each of the five locations (Nittedal, Trondheim, Bodø, Tromsø and Gamvik), obtained through the webpage SunCalc. We then used the light-measurements from Nittedal and Trondheim to estimate light-levels at the three remaining locations, averaging light-levels measured in Nittedal and Trondheim for similar sun altitude levels across the daily cycle for each of the three other locations. We then converted the estimated light-level cycles into predation threat values for Bodø, Tromsø and Gamvik, as described above. Figure S1.6 shows the estimated predation threat cycles for each of the five locations (not showing the added effect of energy reserves on predation threat, see Methods and Fig. 1d). Fifth degree polynomial model equations describing the temporal predation threat for each location are defined with equations S1.13 to S1.17 below.

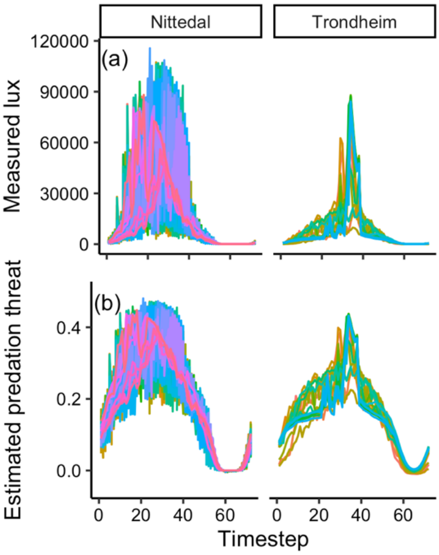

Figure S1.5: Daily cycles of light or light-dependent predation threats between sunrise and the following sunrise (one timestep corresponds to 20 minutes) for Nittedal and Trondheim in July. **(a)** The measured light levels (lux) at each location across the day and night. **(b)** Estimated predation threat at the two locations, converted from the measured light-levels as described in equation S1.6.

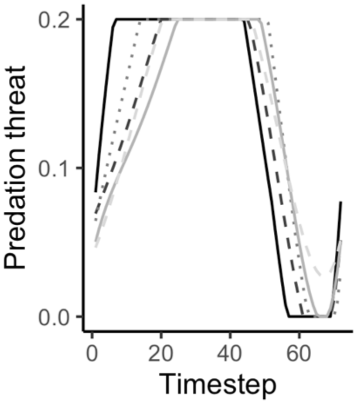

Figure S1.6: Estimated predation threat cycles for each of the five locations based upon light-measurements and sun altitudes, here shown with conditions of maximum values of 0.2 and minimum values of 0.0001. Cycles for each location is shown as listed: Nittedal as black solid line; Trondheim as dark grey dashed line; Bodø as grey dotted line; Tromsø as light grey solid line; Gamvik as light grey dashed line.

Nittedal:
$$0.06 + 0.03 \times t - 8.09 \times 10^{-4} \times t^2 + 1.29 \times 10^{-5} \times t^3 - 2.59 \times 10^{-7} \times t^4 + 2.26 \times 10^{-9} \times t^5 \text{ if } t < 52;$$
$$0.28 + 0.026 \times t - 8.83 \times 10^{-4} \times t^2 + 1.28 \times 10^{-5} \times t^3 - 2.56 \times 10^{-7} \times t^4 + 2.38 \times 10^{-9} \times t^5 \text{ if } t \geq 52 \tag{S1.13}$$

Trondheim:
$$0.06 + 0.006 \times t - 4.95 \times 10^{-5} \times t^2 + 1.18 \times 10^{-5} \times t^3 - 4.35 \times 10^{-7} \times t^4 + 3.67 \times 10^{-9} \times t^5 \tag{S1.14}$$

Bodø
$$0.052 + 0.012 \times t - 3.3 \times 10^{-4} \times t^2 + 2.25 \times 10^{-5} \times t^3 - 6.36 \times 10^{-7} \times t^4 + 4.91 \times 10^{-9} \times t^5 \tag{S1.15}$$

Tromsø
$$0.040 + 0.011 \times t - 6.92 \times 10^{-4} \times t^2 + 3.89 \times 10^{-5} \times t^3 - 8.52 \times 10^{-7} \times t^4 + 5.79 \times 10^{-9} \times t^5 \tag{S1.16}$$

Gamvik
$$0.041 + 0.006 \times t + 2.13 \times 10^{-4} \times t^2 - 3.84 \times 10^{-6} \times t^3 - 1.06 \times 10^{-7} \times t^4 + 1.44 \times 10^{-9} \times t^5 \tag{S1.17}$$

1.2.5 Light-dependent energetic competition cost

Predation threat is not the single potential explanation of the evolved nocturnality of insectivorous bats, and three main alternative hypotheses have been presented and debated, these being overheating, competition from insectivorous birds and mobbing by non-competitors. Although strong support for these hypotheses have proven difficult to obtain through field-observations and lab-experiments (Speakman 1991b; Speakman 1995; Speakman *et al.* 2000), there are likely complex relationships regarding daylight activity costs for insectivorous bats that does not solely involve the risk of being predated upon. We therefore added a second light-dependent cost to our model framework, this being an energetic cost rather than a direct fitness cost, to account for potential direct or indirect energy expenditure caused by interspecific competition or mobbing by birds. We used the measured or estimated daylight cycles as described in section 1.2.4 above and converted the values as described in equation S1.18 (below) to generate what we considered to be realistic value-ranges (see Supplementary Materials 2), although with an implemented higher threshold of 0.2 due to assumptions of the energetic competition cost becoming light-independent above certain values (Fig. S1.7).

$$\text{Energetic competition cost:} \quad = \frac{(\log(\text{lux}))^{1.8}}{70} \quad . \qquad \text{(S1.18)}$$

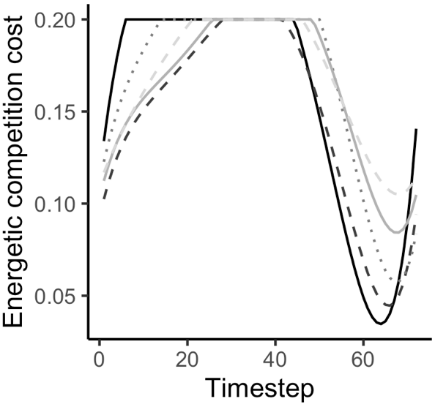

Figure S1.7: Estimated competition cost cycles for each of the five locations based upon light-measurements and sun altitudes, here shown with conditions of maximum values of 0.2. Cycles for each location is shown as listed: Nittedal as black solid line; Trondheim as dark grey dashed line; Bodø as grey dotted line; Tromsø as light grey solid line; Gamvik as light grey dashed line.

Fifth degree polynomial model equations describing the temporal energetic competition cost for each location are defined with equations S1.19 to S1.23 below.

Nittedal: 0.11 g + 0.02 × t – 0.001 × t^2 + 4.72 × 10^{-5} × t^3 - 8.34 × 10^{-7} × t^4 + 5.31 × 10^{-9} × t^5 (S1.19)

Trondheim: 0.09 g + 0.01 × t - 7.48 × 10^{-4} × t^2 + 3.24 × 10^{-5} × t^3 - 6.29 × 10^{-7} × t^4 + 4.10 × 10^{-9} × t^5 (S1.20)

Bodø 0.11 + 0.012 × t - 7.35 × 10^{-4} × t^2 + 3.13 × 10^{-5} × t^3 - 6.13 × 10^{-7} × t^4 + 3.98 × 10^{-9} × t^5 (S1.21)

Tromsø 0.10 + 0.01 × t - 7.12 × 10^{-4} × t^2 + 3.06 × 10^{-5} × t^3 - 5.73 × 10^{-7} × t^4 + 3.59 × 10^{-9} × t^5 (S1.22)

Gamvik 0.11 + 0.006 × t – 1.99 × 10^{-4} × t^2 + 8.12 × 10^{-6} × t^3 - 1.92 × 10^{-7} × t^4 + 1.4 × 10^{-9} × t^5 (S1.23)

Supplementary Materials 2: Linear interpolation

Because the energetic state variable (x) used for calculating fitness values is a discrete rather than a continuous variable, the model needs to specify how the model calculates corresponding fitness values from energetic values that fall in-between discrete steps. For this framework we have implemented the interpolation method described in Clark and Mangel (2000). Here, the model assumes that there is a linear increase in the fitness values from one discrete energetic reserve value to the next. For a current energetic reserve value (x) that does not correspond to one of the specified discrete integers (j), we can specify the following linear interpolation functions (as described in Clark & Mangel 2000):

$$\mathrm{Fit}(x_c, y, w, t, d) = V(x, y, w, t, d)\ . \tag{2.1}$$

If $$j \le x_c < j + 1 \quad , \tag{2.2}$$

then $$\Delta x = x - j \quad , \tag{2.3}$$

then $$V(x, y, w, t, d) = \mathrm{Fit}(x_c, y, w, t, d) \cong \begin{cases} (1 - \Delta x_c) Fit(j, y, w, t, d) + \Delta x_c Fit(j + 1, y, w, t, d) & \text{if } j < j_{max} \\ Fit(j_{max}, y, w, t, d) & \text{if } j = j_{max} \end{cases} \ . \tag{2.4}$$

Supplementary Materials 3: Parameter adjustments

Some parameter values were not possible to obtain or verify from the literature, because they lack any previous quantification. This included the parameters for predation threat, energetic competition cost and resting benefit. However, we judged these parameters to be important for our model system based upon assumptions regarding drivers of general bat behaviour (see Discussion in main text), and therefore felt we needed to attempt to include more-or-less realistic values followed by sensitivity tests where we tested the consequences in our model system if the values were increased or decreased (Fig. S3.1-11). Both the predation threat and the competition costs were based on light-measurements (see Supplementary Materials 1), and thus follow the established daily cycle but further testing was required to arrive at the most reasonable and hopefully realistic values. The resting fitness benefit was assumed to be time and temperature independent and thus kept as a simple non-static value.

Figures S3.1-S3.11 show the summary plots of daily decisions from 'forward' simulations of 200 individuals across 30 days for Nittedal and Trondheim, revealing the results of different parameter values (within figures) across day types (between figures). We carried out evaluations of each of the three parameters as described below.

Figures S3.1-S3.11 show that the removal of the benefit of resting over torpor ($\theta = 0$) resulted in no resting behaviour being expressed across any day type or location. Because bats have been found capable of using heat generated from initiating flight to finalise their rewarming process from torpor (Willis & Brigham 2003), bats in our model were not required to enter a resting state between being torpid and going out to forage, and could thus go directly from being torpid to foraging, although they still had to pay the temperature-dependent rewarming cost when carrying out this transition. With no benefits of being awake, resting behaviour was thus never expressed in our model even on warm days. An enlarged resting benefit ($\theta = 0.003$), however, led to excessive amounts of time spent resting during day and night on any of the warm day types (Fig. S3.1-3 and S3.6-9). Given the other known baseline values (Table 1 in the Methods main text), a resting benefit of 0.0015 was thus considered most representative. This is because patterns where the bats spend most of the day awake and resting are usually associated to unusual and excessively warm days (corresponding to 'very warm' day types in our model framework) in non-reproductive individuals (see Turbill *et al.* 2003).

Alterations of either side of baseline levels of predation threat also led to less realistic outcomes. A decrease in predation threat (μ - 0.03) resulted in bats leaving the roost to forage long before sunset, while an increase (μ + 0.03) resulted in delaying the onset of foraging until long after sunset while experiencing high mortality from predation, especially in the Trondheim scenario.

Adjusting the energetic competition cost (assuming this is caused by interspecific competition from diurnal insectivorous birds or energy expenditure from avoiding mobbing by crows or other birds) led to alterations in the amount of time spent resting and foraging on days and nights across day types. With no competition cost implemented in the model ($C = 0$), the bats spent excessive amounts of time resting and foraging, even on some of the colder day types. An increase in the energetic competition cost (C + 0.05), on the other hand, led to a drastic reduction in time spent foraging and resting on any of the warm day types at either location. Even on 'very warm' days did the bats spend a considerable part of the morning torpid with this adjusted scenario.

Like any other parameter from the baseline scenarios (Table 1 in Methods), the values used in our model may not be representative for any specific bat population at any particular habitat or latitude, but as a general model framework for high-latitude living bats we believe these previously non-quantified relative values are very likely to be within realistic ranges.

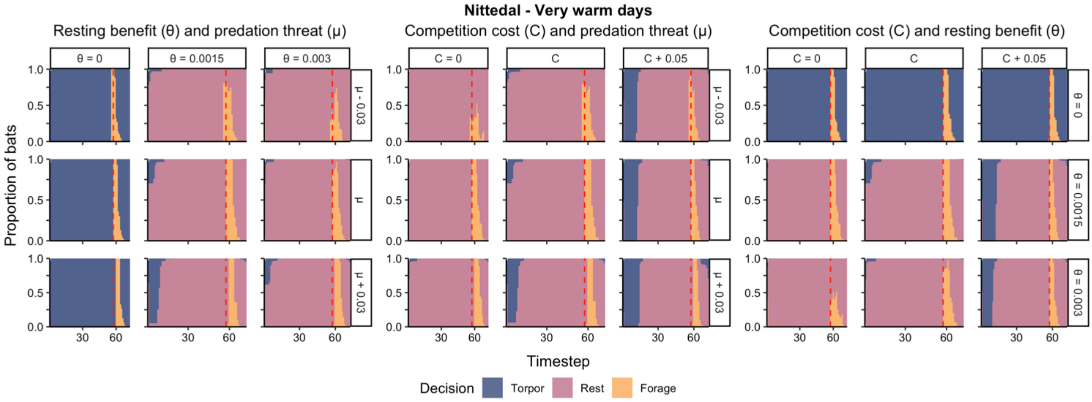

Fig. S3.1: Summary plots of all individual activity decisions across the daily cycle (from sunrise to following sunrise) for 'very warm' days in Nittedal from the forward iterations. Each pane represents one summary plot for given values of resting benefits (*θ*), predation threats (*μ*) and competition costs (*C*). The three parameters are tested pairwise, with the third parameter kept at baseline levels. The plots illustrate how an increase (right and bottom panes) or a decrease (left and top panes) in these parameter values affect daily activity patterns in bats. Red dashed vertical lines indicate the timing of sunset.

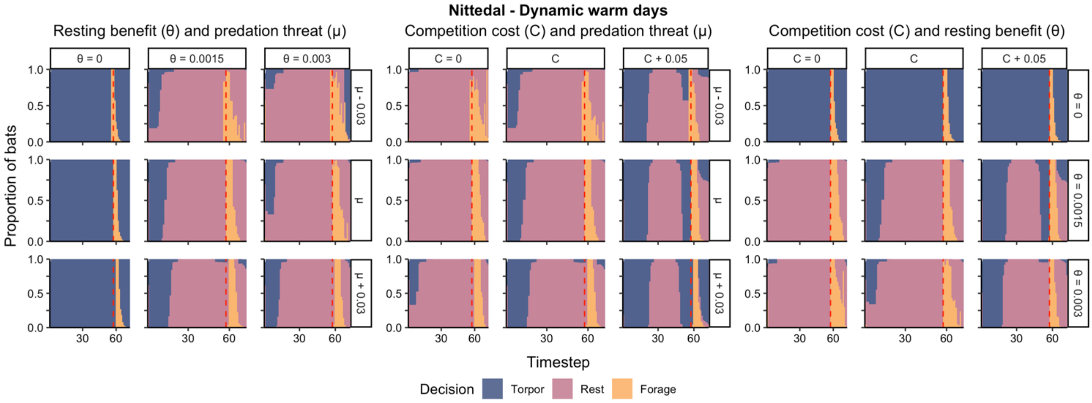

Fig. S3.2: Summary plots of all individual activity decisions across the daily cycle for 'dynamic warm' days in Nittedal from the forward iterations.

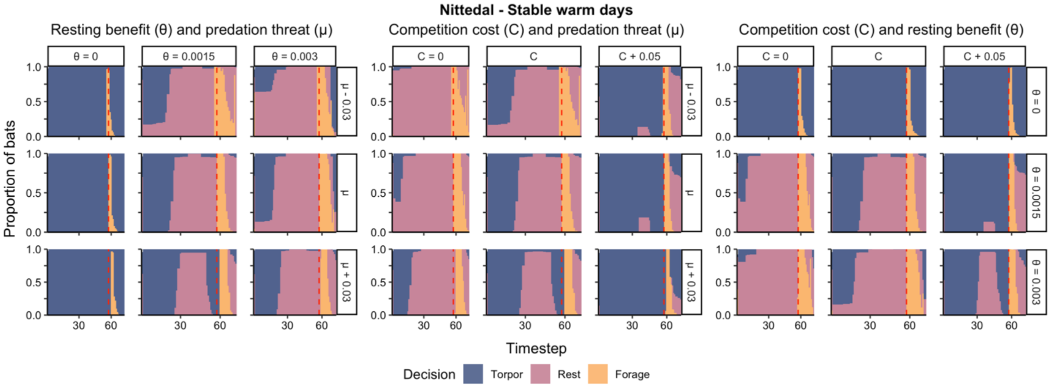

Fig. S3.3: Summary plots of all individual activity decisions across the daily cycle for 'stable warm' days in Nittedal from the forward iterations.

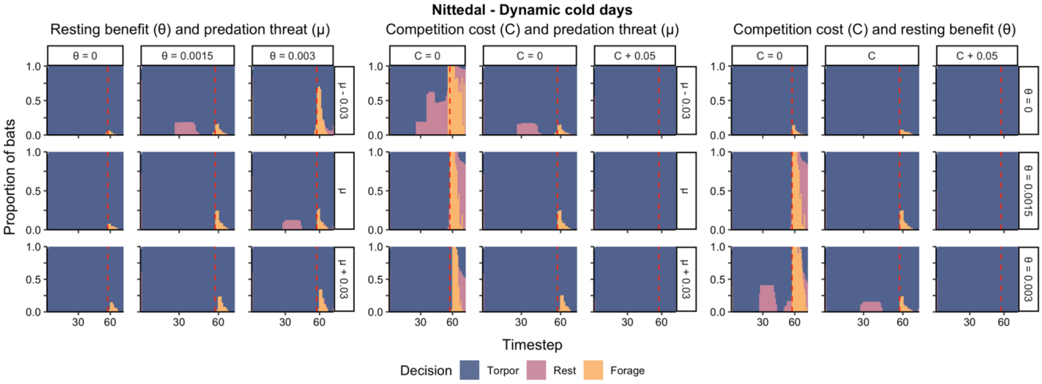

Fig. S3.4: Summary plots of all individual activity decisions across the daily cycle for ‘dynamic cold’ days in Nittedal from the forward iterations.

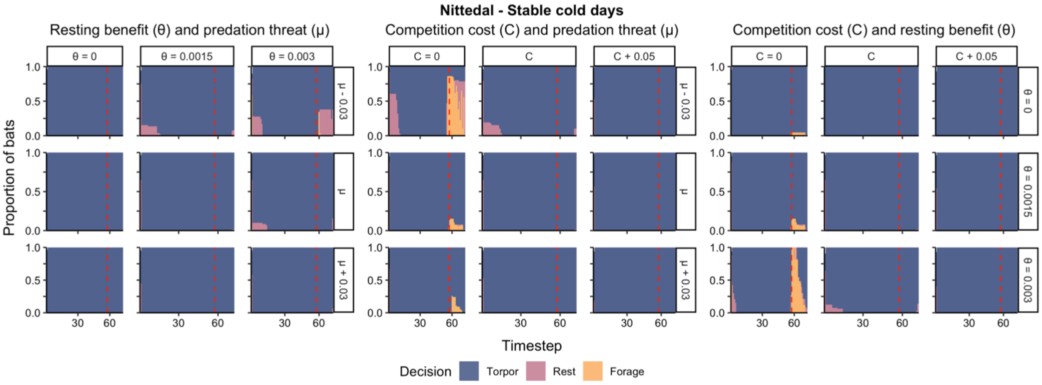

Fig. S3.5: Summary plots of all individual activity decisions across the daily cycle for ‘stable cold’ days in Nittedal from the forward iterations.

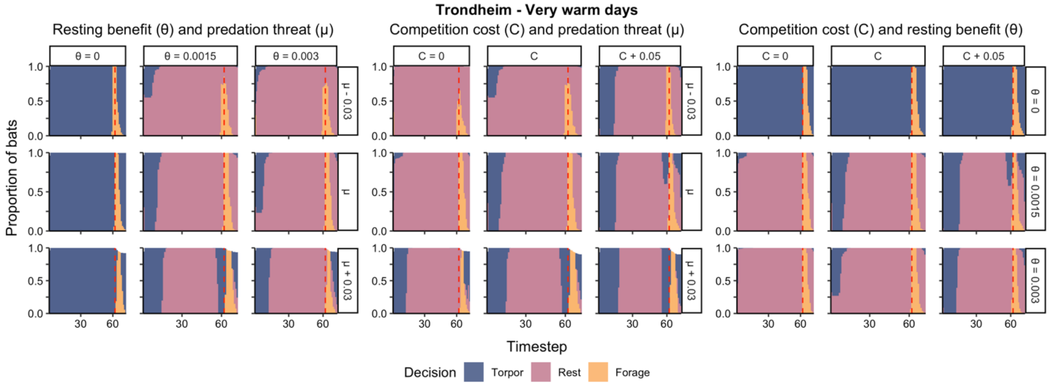

Fig. S3.6: Summary plots of all individual activity decisions across the daily cycle for ‘very warm’ days in Trondheim from the forward iterations.

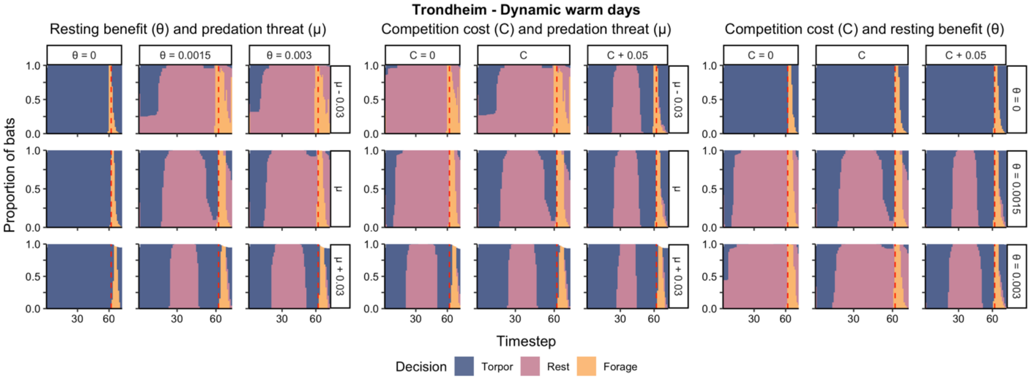

Fig. S3.7: Summary plots of all individual activity decisions across the daily cycle for ‘dynamic warm’ days in Trondheim from the forward iterations.

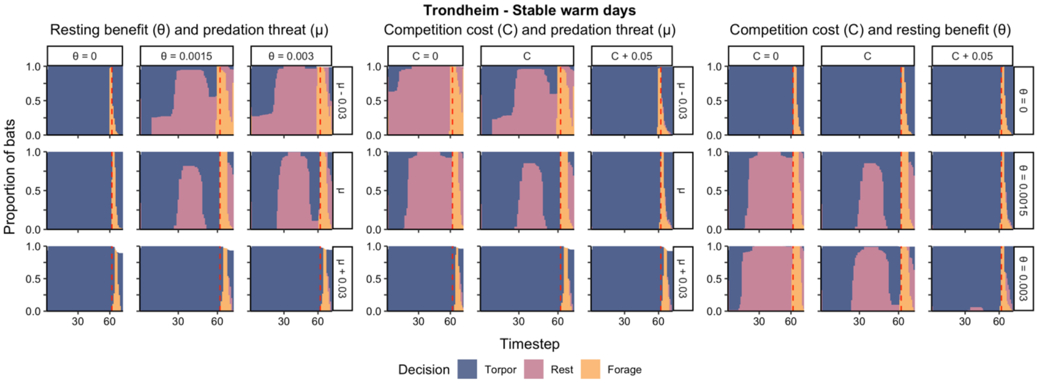

Fig. S3.8: Summary plots of all individual activity decisions across the daily cycle for ‘stable warm’ days in Trondheim from the forward iterations.

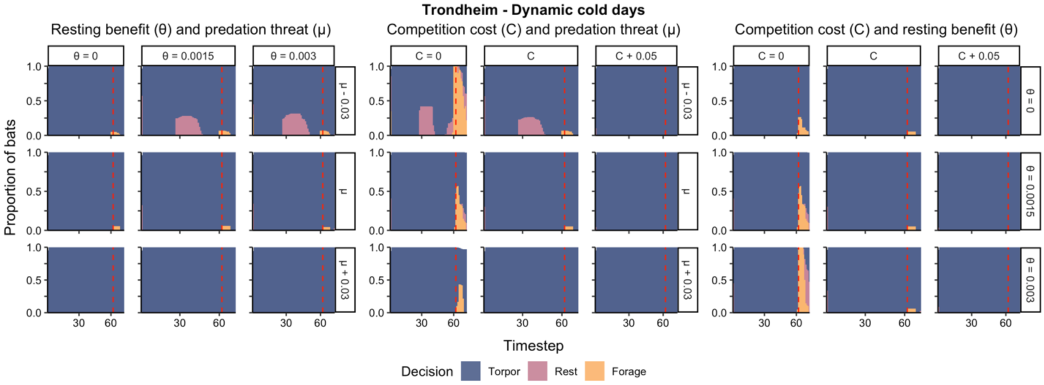

Fig. S3.9: Summary plots of all individual activity decisions across the daily cycle for ‘dynamic cold’ days in Trondheim from the forward iterations.

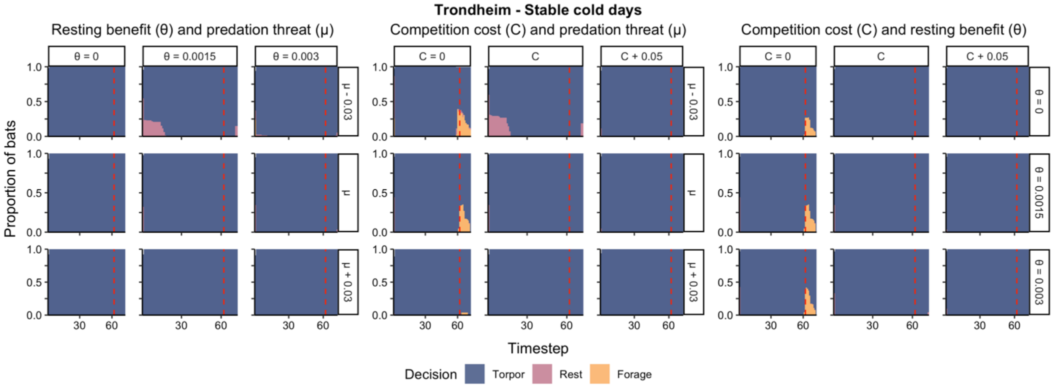

Fig. S3.10: Summary plots of all individual activity decisions across the daily cycle for ‘stable cold’ days in Trondheim from the forward iterations.

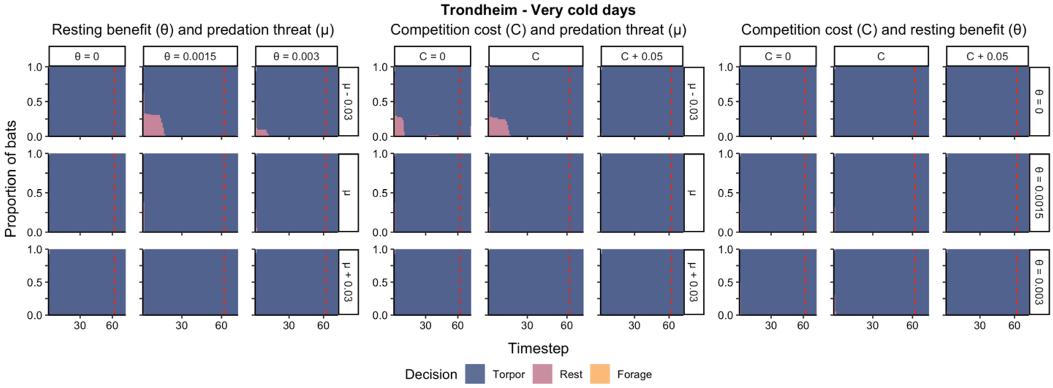

Fig. S3.11: Summary plots of all individual activity decisions across the daily cycle for ‘very cold’ days in Trondheim from the forward iterations.

Supplementary Materials 4: Fat reserves across the daily cycle

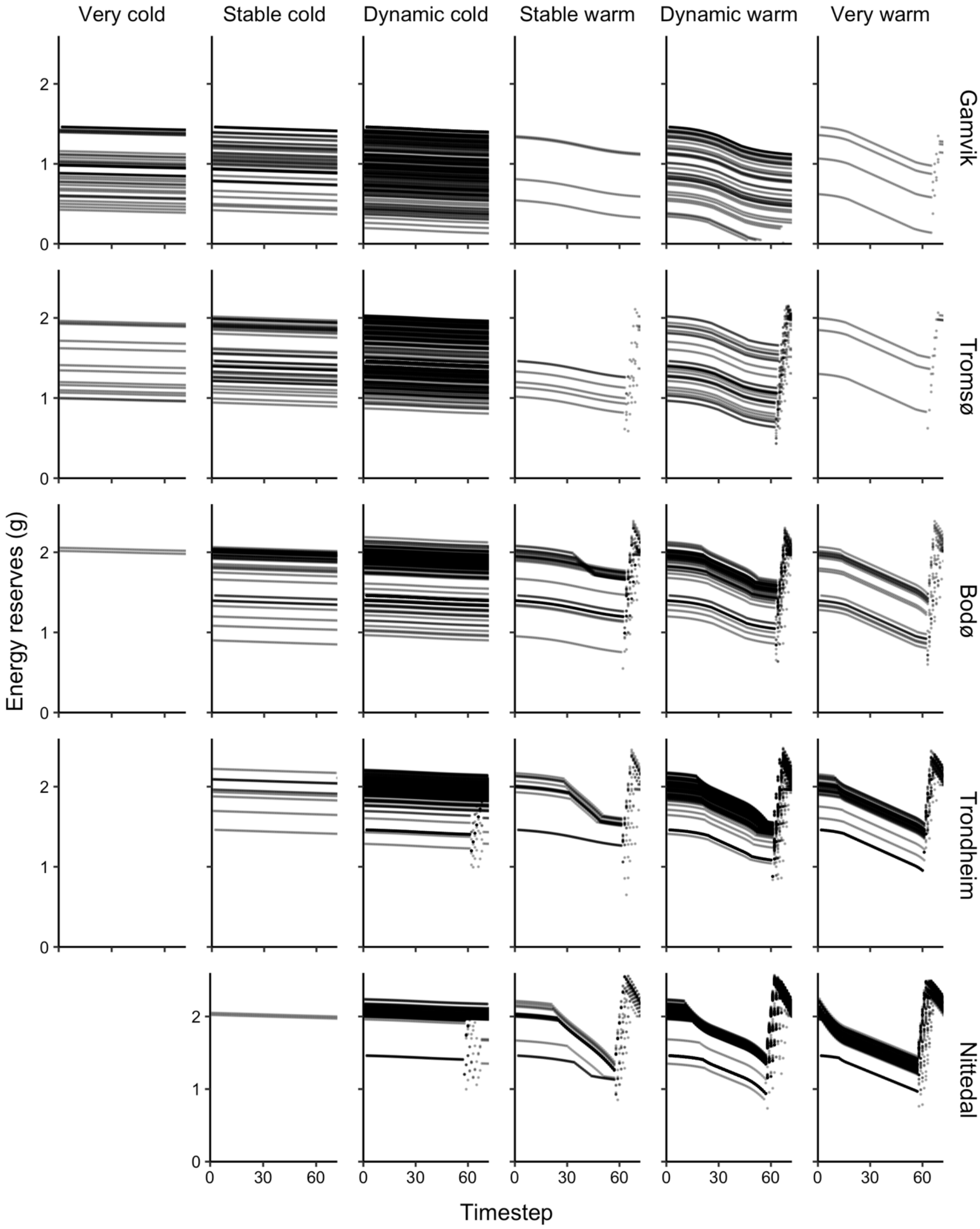

Figure S4.1: Summary plots of all individual fat reserves across the daily cycle (from sunrise to following sunrise) extracted from the forward iterations with baseline values across day types in the Nittedal, Trondheim, Bodø, Tromsø and Gamvik scenarios. Given the different probabilities for each day type at each location, the number of individual trajectories vary between day types and locations (the day type 'very cold' days had an occurrence probability = 0 in the Nittedal scenario and is thus not shown in the figure).

Supplementary Materials 5: Empirical data comparisons

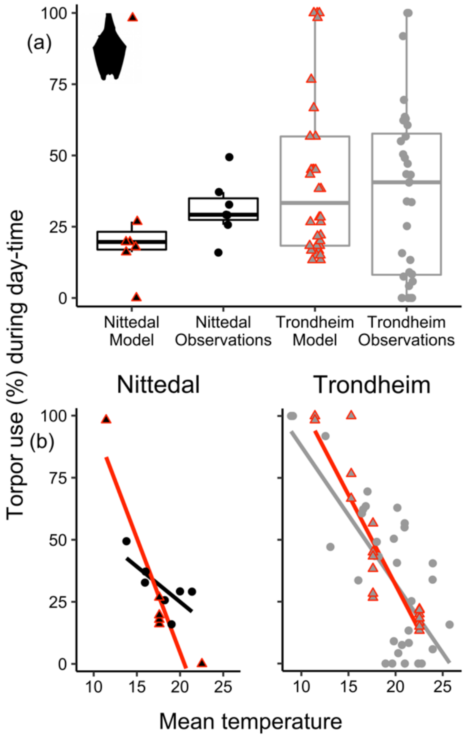

Figure S5.1: Comparisons of day-time torpor use (%) from field derived data (round points) and from model simulations (triangle points with red outline) for the two locations of Nittedal (black points and boxes) and Trondheim (grey points and boxes). **(a)** Boxplots of daily torpor use between locations and data origin with boxes marking the data median and the 25th and 75th percentiles. **(b)** Negative effects of increasing mean daily temperatures on day-time torpor expression, both in the empirical data (round points and black or grey lines) and in data generated from matched simulated model runs (triangle points and red lines).

Table S5.1: Means and ranges of the percentages of day-time and night-time behaviour in the empirical data and from the model simulations at the two locations Nittedal and Trondheim.

	Nittedal		Trondheim	
	Empirical data	Model simulations	Empirical data	Model simulations
Daily torpor use				
Mean time (± sd)	31.3% (±10.3)	29.1% (±31.6)	37.3% (±30.3)	44.0% (±29.7)
Range time	15.9% to 49.4%	0% to 98.2%	0% to 100%	13.3% to 100%
Nightly foraging				
Mean time (± sd)	60.3% (±14.1)	33.0% (±20.0)	39.3% (±30.0)	42.2% (±23.7)
Range time	32.3% to 74.2%	0% to 62.5%	0% to 80.8%	0% to 66.7%
Nightly torpor use				
Mean time (± sd)	20.8% (±11.4)	25.9% (±44.6)	34.7% (±39.2)	29.6% (±36.3)
Range time	0% to 32.3%	0% to 100%	0% to 100%	0% to 100%
Nightly resting				
Mean time (± sd)	18.9% (±10.8)	41.1% (±29.9)	24.0% (±18.8)	28.2% (25.2%)
Range time	0% to 35.5%	0% to 68.8%	0% to 58.3%	0% to 66.7%

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Paper IV

Physiological and behavioural strategies of brown long-eared bats in summer at high-latitudes: torpor, foraging times and effects of reproductive condition

Mari Aas Fjelldal[1*], Jonathan Wright[1], Rune Sørås[1] & Clare Stawski[1,2]

[1]*Department of Biology, Norwegian University of Science and Technology (NTNU), 7491 Trondheim, Norway*
[2]*School of Science, Technology and Engineering, University of the Sunshine Coast (USC), Maroochydore DC, Queensland, 4558, Australia*

Abstract

Nocturnal animals living at high latitudes face energetic challenges during mid-summer given the limited number of night time hours available to forage. Insectivorous bats cope with these challenges by expressing torpor to save energy while roosting, despite the physiological and ecological costs of heterothermy, especially for pregnant and lactating females. In this study, we investigated heterothermic strategies and behavioural foraging patterns using roosting skin temperature data from 39 brown long-eared bats (*Plecotus auritus*) in different reproductive states over 288 days, close to their northern distributional limit in Norway. At the population level, deep and frequent torpor use was confirmed to be an important strategy for managing daily energy budgets, although lactating females expressed less torpor during the day and pregnant females mainly entered only shallow torpor bouts. As predicted from earlier state-dependent modelling, the strategic use of torpor was dependent upon time of day, temperature, barometric pressure, rainfall, humidity, individual sex and roost type, although ambient temperature was always the strongest predictor. Bats delayed start of evening foraging trips on lighter nights, typically emerging from the roost only when light levels decreased below 6 lux (median light level at emergence = 1.5 lux), likely because higher light levels are associated with increased predation risk. However, no such effect was found in morning return times to the roost, for which bats showed considerably greater light-tolerance (median light level at return = 173.5 lux). Lactating females, however, took apparently higher risks and left the roost approximately 25 minutes earlier than non-reproductive individuals, presumably because of their greater energetic requirements and limited ability to save energy using torpor. These results further add to our understanding of how bats at high latitudes cope with restricted summer foraging times and energetically expensive reproduction by strategically adjusting their daily behavioural and thermoregulatory schedules according to short-term changes in their local environment.

Keywords: torpor; heterothermy; *Plecotus auritus*; light sensitive; radio telemetry; diurnal routines; foraging schedules