Received: 31 July 2020 | Accepted: 1 November 2020

DOI: 10.1111/1365-2435.13718

Functional Ecology BRITISH ECOLOGICAL SOCIETY

REVIEW

A unifying, eco-physiological framework for animal dormancy

Kathryn Wilsterman[1,2] | **Mallory A. Ballinger**[2] | **Caroline M. Williams**[2]

[1]Biological Sciences, University of Montana, Missoula, MT, USA

[2]Integrative Biology, University of California, Berkeley, CA, USA

Correspondence
Kathryn Wilsterman
Email: kathrynwilsterman@gmail.com

Funding information
NSF Division of Graduate Education, Grant/Award Number: 1106400; NSF Division of Integrative Organismal Systems, Grant/Award Number: 1558159; NSF Division of Biological Infrastructure, Grant/Award Number: 1907233

Handling Editor: Jean-François Lemaître

Abstract

1. Various animals across the tree of life express some form of programmed dormancy (e.g. hibernation, diapause) to maximize fitness in highly seasonal environments. The integrated phenotype of animals undergoing programmed dormancy is strikingly similar among diverse groups; however, research on programmed dormancy has historically been phylogenetically siloed. A broad comparative approach could clarify new angles for answering fundamental questions about programmed dormancy evolution.
2. To advance this approach, we present a cross-taxonomic framework describing dimensions that distinguish animal dormancies and provide a set of core traits that animals regulate as they progress through the eco-physiological phases of deep, programmed dormancy.
3. We use this universal framework to explore the ultimate drivers and evolutionary consequences of dormancy across the tree of life. Deep, programmed dormancy appears to be a predictable and repeated adaptation to highly seasonal environments that draws on a conserved suite of ancestral traits. We highlight evidence for molecular convergence in signalling pathways coordinating environmental sensing and energy metabolism in the insect and mammal lineages, separated by 700 million years of evolution and representing independent colonizations of highly seasonal environments.
4. Lastly, we discuss the utility of this new framework and highlight opportunities and challenges for researchers to continue advancing our understanding of dormancy through a broad, comparative lens.

KEYWORDS

diapause, hibernation, hypometabolism, metabolic suppression, seasonality, torpor, winter

1 | INTRODUCTION

Across the tree of life, the term 'dormancy' is used to describe physiological adjustments that enhance survival in temporarily hostile environments (Cáceres, 1997; Geiser, 1998; Hand, 1991; Koštál, 2006). Dormancies have been documented in all animal phyla except Echinodermata (Hand, 1991), and are described using a wide variety of taxon-specific names and definitions (Table 1). Within and among these groups, dormancies span an extremely broad range of physiological states, from the nearly inert, 'latent life' state called cryptobiosis exemplified by Tardigrades (Jönsson et al., 2019) to more subtle state of hypometabolism exhibited by some active high latitude ungulates (in winter; Arnold, 2020) and polar bears (in summer; Nelson et al., 1983; Whiteman et al., 2015).

Animals undergoing different types of dormancies resemble one another in how behaviour, energy metabolism and environmental sensing are regulated, and these processes are often underpinned by deeply conserved regulatory pathways (Hand et al., 2016). Despite these striking similarities, dormancy research is strongly phylogenetically siloed, with little crosstalk among fields in the primary literature (Box 1). The phylogenetic siloing of these closely related research fields inhibits our ability to answer evolutionary,

TABLE 1 Glossary of terminology used to refer to animal dormancies across and among taxa

Term	Taxa	Definition	Citation
Aestivation	Vertebrates and invertebrates	'a state of aerobic hypometabolism that is probably best described as a survival strategy for dealing with arid conditions, but is also typically associated with lack of food availability and frequently with high environmental temperatures'	Storey (2002)
	Birds and Mammals	'torpor in summer/at high ambient temperatures'	Geiser (2010)
Brumation	Ectotherms	'The winter dormancy that is observed in ectothermic species, [in which] animals are dependent on the temperature of their surroundings and are forced to stay torpid until temperatures rise'	Wilkinson et al. (2017)
	Reptiles	'winter dormancy in ectothermic vertebrates that demonstrate physiological changes which are independent of body temperature'	Mayhew (1965)
	Amphibians	'The pre-winter reduced activity and reduced metabolic rates of poikilotherrms'	Borzée et al. (2019)
Daily heterothermy or torpor	Birds and Mammals	A maximum torpor bout duration of less than 24 hr with consistent association with the circadian rhythm of body temperature; a minimum metabolic rate during torpor of >0.1 ml O_2 g^{-1} hr^{-1} and a minimum body temperature above 10°C	Ruf and Geiser (2015)
	Birds and Mammals	Torpor 'lasting for several hours during the rest phase'	Geiser (2013)
Diapause	Animals	'a programmed arrest of development … that may or may not be associated with some degree of metabolic depression'	Hand et al. (2016)
	Invertebrates	'[a dormancy] maintained by an internal physiological responses rather than an external environmental factor'	Cáceres (1997)
	Insects	'A more profound, endogenously and centrally mediated interruption that routes the developmental programme away from the direct mophogenesis into an alternative diapause programmed of succession of physiological events; the state of diapause usually precedes the advent of adverse conditions and the end of diapause need not coincide with the end of adversity'	Koštál, (2006)
	Insects	'an environmentally preprogrammed period of arrested development, characterized by metabolic depression that can occur during any stage of insect development''	Hahn and Denlinger (2011)
Dormancy	Animals	'Dormancy describes a state of reduced (but not complete lack of) metabolism, i.e., hypometabolism'	Withers and Cooper (2010)
	Insects	'A generic term covering any state of suppressed development (developmental arrest) which is adaptive (that is ecologically or evolutionarily meaningful and not just artificially induced), and usually accompanied with metabolic suppression'	Koštál (2006)
	Invertebrates	'An all-encompassing term that includes any form of resting stage, regardless of cues required for induction or termination'	Cáceres (1997)
Hibernation	Animals	'A general term applied to all animals that seek a local refuge (a hibernaculum) in which to overwinter'	Ultsch (1989)
	Insects	A type of diapause entered 'in polar and temperate regions'	Koštál et al. (2017)
	Reptiles	'the general reduction in activity … following cold-acclimation or cold-acclimatization … equivalent to brumation'	Gatten (1978)
	Birds and Mammals	A maximum torpor duration of more than 24h, with strong suppression or even complete arrest of the circadian clock; a minimum metabolic rate in torpor of <0.1 ml O^2 g^{-1} hr^{-1} and a minimum body temperature below 10°C	Ruf and Geiser (2015)
	Birds and Mammals	'Multiday torpor predominantly throughout winter'	Geiser (2013)
	Mammals	A 'strategy for winter survival [in which] animals sink into a deep torpor where metabolic rate is <5% of normal, body temperature falls to 0–5°C, and physiological function are strongly suppressed'	Storey (2003)
Quiescence	Invertebrates	'[a dormancy] Induced and maintained by adverse environmental conditions; includes hibernation, estivation, anhydrobiosis, and cryptobiosis'	Cáceres (1997)
	Insects	'direct inhibition of development by conditions below or above developmental thresholds … [quiescence is] an immediate response (without central regulation) to a decline of any limiting environmental factor(s) below physiological thresholds with immediate resumption of the processes if the factor(s) rise above them'	Koštál (2006)

BOX 1 A phylogenetic siloing of fields studying programmed dormancy

We searched ISI Web of Science on 11 April 2019 for studies from 1900 to 2019 that incorporated ideas from more than one taxonomic (animal) group as a central part of their work (see Appendix 1 in Supporting Information for methods of our literature search). Of 13,223 primary literature studies on diapause, hibernation or brumation, only five studies (Appendix 1, Table S2) set their study in the context of more than one type of animal dormancy according to our criteria. These five studies were focused on either insects or killifish, and our search did not reveal any primary literature on mammalian hibernation that included reference to either brumation or diapause. By using insights from other taxa, these studies illustrate that many shared gene expression and metabolic pathways regulate programmed dormancy across taxa, but the precise wiring of those pathways often differs (Duerr & Podrabsky, 2010; Kučerová et al., 2016; Wang et al., 2018; Xu et al., 2012). It is striking that cross-taxon synthesis in the primary literature has only begun to appear in the past decade. This almost complete siloing of research fields is restricting progress in many areas of research. The siloing of fields is less apparent in the secondary literature (e.g. reviews and syntheses), where researchers have repeatedly emphasized striking similarities in dormancy across animal taxa (Baumgartner & Tarrant, 2017; Hahn & Denlinger, 2011; Hand et al., 2016; Lyons et al., 2013; Malan, 2014; Melvin & Andrews, 2009; Ruf & Geiser, 2015; Schiesari & O'Connor, 2013; Secor & Carey, 2016; Staples, 2016; Storey & Storey, 2004, 2013; Ultsch, 1989). However, this has yet to be fully taken-up by the primary research literature.

ecological, and mechanistic questions about dormancy. For example, ecological and mechanistic similarities among taxa may offer fundamental insight into how natural selection shapes dormancy evolution. Phylogenetic siloing also means parallel research questions and discoveries are more likely to go unrecognized in adjacent fields. Researchers are likely missing opportunities to cross-pollinate hypotheses and research approaches. Unifying these fields has the potential to advance research on both mechanisms and evolution of dormancy.

Because these research fields have been phylogenetically siloed almost since their inception, the concepts and terminology used in each field are also taxon-specific and difficult to apply broadly. Dormancy is often conceptually divided into two discrete ‘types’ (Andrewartha, 1952; Cáceres, 1997; Hand, 1991; Koštál, 2006; Levesque et al., 2016), but the defining features that delineate the dichotomy are taxon-specific and have been the subject of considerable controversy. In the insect literature, dormancy is generally classified as quiescence or diapause, which can be differentiated principally by the role environmental cues play in controlling onset and completion of dormancy (Table 1). In the mammalian and bird literature, the dichotomy is set between daily torpor and hibernation, which are generally differentiated by the duration and magnitude of metabolic suppression (Table 1; Ruf & Geiser, 2015). Some aspects of these definitions do not translate well across taxa, and the dichotomy-driven view of dormancies has proved too rigid to adequately describe the diverse dormancies that exist within a single taxonomic group. In the insect literature, the wide range of variation in the control of the initiation and termination of dormancy lead to debates about whether specific dormancies qualify as ‘diapause’, particularly given that many insects with a dormancy characterized as diapause transition to a state known as post-diapause quiescence relatively early in winter (Hodek, 2002), and may have considerable variation in the degree of suppression in processes such as locomotion, growth, and even development (Koštál et al., 2000; Tatar & Yin, 2001). In the mammalian literature, metabolic flexibility in protoendothermic species (e.g. tenrecs or tropical and sub-tropical bats) that use a mix of daily torpor- and hibernation-like strategies across the heterothemic period have been difficult to integrate with the broader daily torpor-hibernation dichotomy (Nowack et al., 2020; Treat et al., 2018; van Breukelen & Martin, 2015). We need a flexible concept of dormancy that transcends phylogenetic divisions and captures ecologically relevant axes of dormancy to facilitate phylogenetically broad comparative dormancy research.

With this goal in mind, we propose a universal framework comprised of three components—axes, core traits and phases of dormancy—that can be used to classify, compare and contrast dormancies across animal taxa. We illustrate how this framework can be used to explore commonalities in the evolutionary/ecological drivers and consequences of dormancy. Finally, we highlight opportunities for cross-pollination and areas of the proposed framework that will benefit from quantitative expansion. We focus on insects and mammals because the vast majority of research has focused on these taxa and they reflect our research expertise, but we highlight examples from other taxa throughout to illustrate that the framework is generalizable beyond these groups, and we have developed the terminology in consultation with researchers from a wide range of animal dormancy fields. Nonetheless, we acknowledge that others may find that our focus on the big picture commonalities results in oversimplifications and generalizations in some instances.

2 | INTEGRATING ANIMAL DORMANCY RESEARCH IN A UNIVERSAL FRAMEWORK

2.1 | Major axes of dormancy

We suggest that there are three axes that can differentiate dormancy types across animal taxa (Figure 1a). The first two axes, **Induction** and **Recalcitrance**, together capture the degree to which the dormancy is endogenously programmed and centrally mediated (i.e.

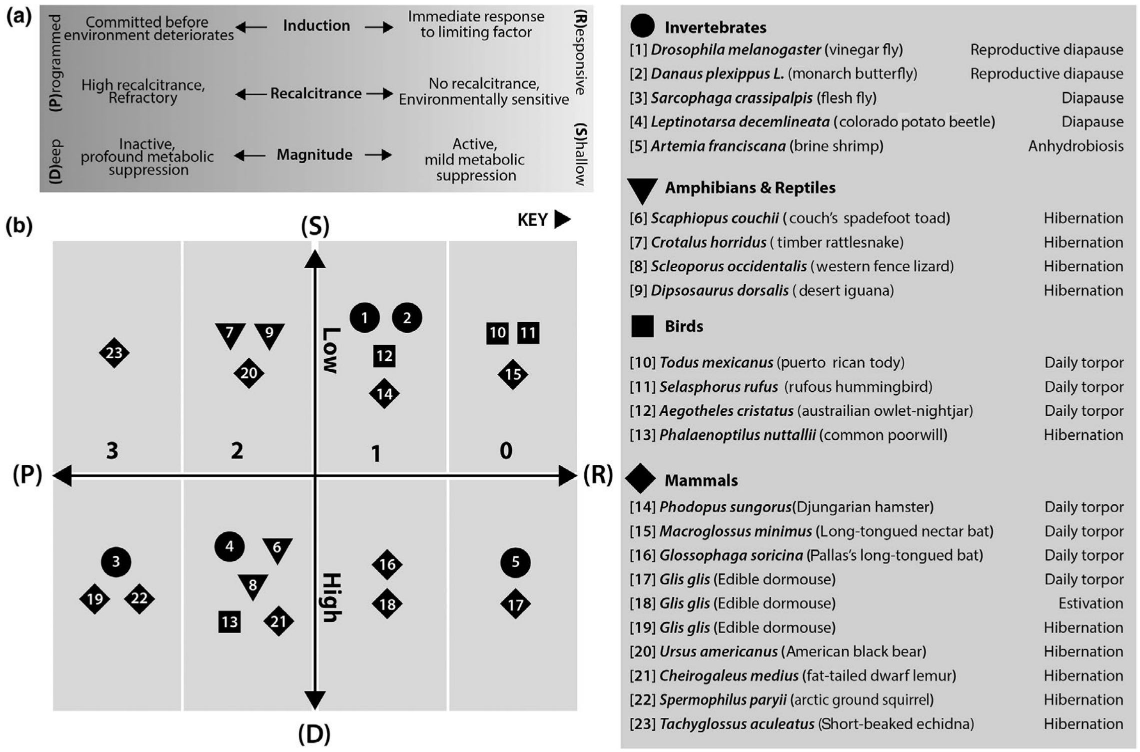

FIGURE 1 The major axes distinguishing animal dormancies. (a) The three axes of dormancy, which differentiate deep, programmed dormancies from shallow, responsive dormancies (see text for further description of axes). (b) Using the framework to classify dormancies of invertebrates, amphibians and reptiles, birds and mammals. We compiled information from the literature on the degree of programming and metabolic suppression (as a measure of magnitude) of representative dormancies for some well-studied dormancy models (Table S4). Some species or individuals may display multiple types of dormancy in different life stages or in response to different environmental challenges, and these dormancies can be compared within the framework as well. *Glis glis* [17, 18, 19] is included here as a well-described example. We collapsed induction and recalcitrance into one axis describing the degree of programming (P = programmed, R = responsive), with grades of 0 (responsive induction, low recalcitrance); 1 (programmed induction, low recalcitrance); 2 (programmed induction and moderate recalcitrance), or 3 (programmed induction, high recalcitrance). We characterized dormancy magnitude (D = Deep, S = shallow) as a dichotomous variable (high/low) based on the degree of metabolic suppression (per cent of basal or standard metabolic rate in a dormant animal compared to a similarly staged non-dormant animal), where high corresponds to >90% for endotherms and >70% for poikilotherms. Note that feeding rate was used in *Drosophila melanogastor* as no metabolic rate data were available. Species key is on the right

driven by central nervous system and endogenous time-keeping mechanisms), versus a direct response to an adverse environment. The third axis, **Magnitude**, describes the dormancy-specific degree of plasticity in a range of traits, including metabolic rate (described fully in Section 2.2).

The **Induction** axis describes the process by which animals are committed to entering the dormancy program, as opposed to continuing the active season lifecycle (Koštál, 2006). Induction of dormancy is classified as responsive when dormancy is initiated immediately and in direct response to a factor (often environmental, such as temperature, water or nutrients) crossing a physiological threshold. For example, food restriction induces spontaneous torpor in deer mice *Peromyscus maniculatus* regardless of season (Tannenbaum & Pivorun, 1984, 1988). Induction is programmed when the animal is committed to entering dormancy prior to the onset of environmental deterioration, often allowing for an extended preparation period during which the animal remodels its physiology and other traits (see Phases of Dormancy). Induction can be programmed in two distinct ways: (a) Obligate dormancies occur at a set life stage (in the case of annual life cycles such as insects) or set time of year determined by the endogenous circannual clock, regardless of environmental conditions (Andrewartha, 1952; Danks, 1987; Harlow & Menkens Jr., 1986; Koštál, 2006; Nelson et al., 2010; Pengelley & Asmundson, 1969); (b) Facultative dormancy occurs only if animals receive the appropriate environmental cues (also known as token stimuli, often photoperiod and temperature; Harlow & Menkens Jr., 1986; Ryan et al., 2018; Tauber & Tauber, 1981; Vornanen et al., 2009) to induce dormancy; if those cues are not detected then the animal will proceed with the active season life cycle. The sensitive period for detecting cues used for facultative induction may occur well in advance of dormancy initiation, or even in the parental generation in insects with more than one generation per year (Denlinger, 1972).

The **Recalcitrance** axis describes the strength of the endogenous lock preventing an animal from breaking dormancy prematurely. An animal with a high degree of recalcitrance will remain in dormancy for weeks, if not months, once the dormancy program is initiated, even if environmental conditions become permissive. High recalcitrance of dormancy ensures that dormancy is not prematurely terminated during a mild spell and may extend beyond the duration of adverse conditions. Experimentally, recalcitrance can be measured as either the time taken or proportion of individuals that resume active season physiology and behaviour after entering dormancy when transferred to or held under permissive conditions (French, 1982; Koštál, 2006; Pengelley & Fisher, 1963; Tauber & Tauber, 1976; Wooding & Hardisky, 1992). Dormancy recalcitrance differs systematically among species and populations (Masaki, 2002), and it also declines as dormancy progresses. As a useful starting point for species- or population-level comparisons, recalcitrance should be measured early in dormancy, ideally immediately after initiation (see Phases). The molecular and physiological mechanisms underlying variation in dormancy recalcitrance (and thus timing of spring emergence) are an active area of research in both mammalian and insect dormancy literature (e.g. (Hut et al., 2014; Powell et al., 2020).

The third axis, **Magnitude**, describes the degree of dormancy-specific plasticity in the core physiological and behavioural traits, relative to a non-dormant animal at a similar life stage. The degree of metabolic suppression is a common metric of dormancy magnitude that is already widely used across taxa (Guppy & Withers, 1999; Ruf & Geiser, 2015). Additional traits such as activity and energy storage allow for a multivariate characterization of magnitude (see Section 2.2).

We chose some well-studied examples of dormancies to illustrate how this framework can provide a semi-quantitative characterization of major dormancies that transcend phylogenetic divisions (Figure 1b). Using this cross-taxonomic framework illustrates that there is a cluster of animals that express deep, programmed dormancies, including representatives from insects, birds, mammals and amphibians. More broadly, we find examples of eutherian dormancies that fall across the full length of each proposed axes, whereas poikilotherms (invertebrates, reptiles and amphibians) are only found in six of these categories, and birds only occupy three. Although endothermy apparently allows for diverse dormancy strategies in eutherians, birds are more constrained. In invertebrates, the degree of programming appears to be more closely linked to the magnitude of the dormancy. Within a dormancy sub-type (e.g. diapause, hibernation) there is a range of variation in both programming and magnitude, and all subtypes cover more than one quadrant. For example, insect diapause includes dormancies ranging from the shallow and relatively responsive reproductive dormancy of *Drosophila melanogaster* [1], to the deep and highly programmed dormancy of *Sarcophaga crassipalpis* [3]. Aestivation generally refers to a responsive dormancy that occurs in response to food or water shortages (Storey & Storey, 2012), but there are reported instances of aestivation that fall within the quadrant of deep, programmed dormancy (see [21, 24]; Bieber & Ruf, 2009; Dausmann et al., 2004; Hoelzl et al., 2015; McNab, 2002). Tropical and sub-tropical dormancies are often characterized by greater flexibility (Dausmann et al., 2004; Faherty et al., 2018; Fietz & Dausmann, 2007; Geiser, 2020; Lovegrove et al., 2014), and thus are classified as more responsive in terms of induction and recalcitrance. Finally, even within a species or individual, dormancies in different life stages, or in response to different environmental challenges, may fall into different quadrants (e.g., see [17, 18, 19]). Additional work is required to develop these into truly quantitative indices, but our capacity to do so depends on cross-talk among fields to facilitate the collection of comparable data across taxa.

2.2 | Core traits and phases of dormancy

In contrast to historic views of dormancy as a state of suspended animation, we know now that the dormant period is a dynamic stage made up of distinct, sequential phases (Carey et al., 2003; Denlinger, 2002; Hand et al., 2016; Hirche, 1996; Koštál, 2006). Animals gradually modify their behaviour, morphology and physiology in predictable, ordered ways as they proceed through dormancy. The second component of our framework is a working model of how the core traits that form the integrated dormancy phenotype are organized and regulated throughout the phases of dormancy (Figure 2). The broad working model we propose here is intended to apply across the animal phylogeny and is thus based on patterns for which there is evidence across taxa. In general, our discussion reflects evidence for the pattern across taxa, but in some instances, there is excellent evidence for the pattern in one taxon but it has only been examined a handful of times in other taxa. Thus, our working model is a hypothesis that should motivate quantitative assessments of its generality (see Section 4 and Box 2). With this in mind, citations throughout this section are intended to be used as starting points for researchers interested in comparative physiology and ecology of dormancy, and thus they may not be exhaustive or comprehensive.

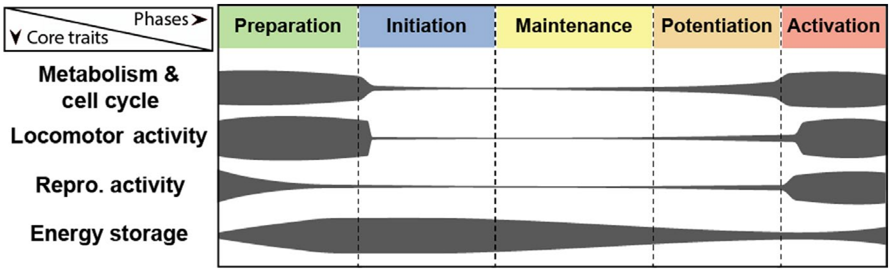

FIGURE 2 Phases and Core Traits of dormancy. During dormancy, animals proceed through distinct phases (columns, described in detail in the text) during which core phenotypic traits (rows) are up-and down-regulated (corresponding to width of grey bands). Adjacent phases may temporally overlap, not all phases occur in all species and trait regulation will vary across species

Here we outline our working model using dormancy literature from a wide range of animal taxa. The first component of this working model is the set of core traits. Core traits refer to quantifiable traits that can provide a multivariate and comparative characterization of how the physiology, morphology and behaviour of an animal undergoing dormancy changes, from active season to active season, thus making up the integrated dormancy phenotype. The most fundamental core traits are a decrease in the cell cycle (in at least some tissues) and metabolic rate during dormancy (compared to a similarly staged non-dormant animal). A decrease in either locomotor activity or reproductive function is also frequently diagnostic in animals that are dormant in otherwise active life stages. Finally, energy storage becomes essential as dormancies increase in their degree of programming (particularly the degree of recalcitrance, which usually underlies dormancies of longer duration).

The second part of our working model organizes the regulation of these core traits into distinct phases that facilitate intra- and interspecific comparisons using biological time rather than calendar time. This is critical because, using only calendar time, dormancy phenology varies geographically according to season length, complicating comparisons of biochemical and physiological data. To overcome this challenge, insect physiologists divided deep, programmed dormancy into a set of eco-physiological phases, which describe sequential modifications to physiology and behaviour that insects undergo during transitions into and out of dormancy (Danks, 1987; Koštál, 2006). Experimental transcriptomic studies support the biological relevance of these phases (Dowle et al., 2020; Koštál et al., 2017). With this utility in mind, our phases of dormancy build on those defined by Koštál (2006) and expand their utility to all animals.

In line with Koštál, the full set of phases are defined using deep, programmed dormancies, in part because these dormancies are the most organized and predictable. All dormancies share the **Initiation** and **Activation** phases, which describe the traditional 'beginning' and 'end' of dormancy proper, but dormancies that are more responsive (lacking induction and/or with low recalcitrance) will lack some phases that are critical for deep, programmed dormancy (e.g **Preparation**). Finally, although these phases and traits are focused on winter dormancies, which are well-studied, we expect tropical and sub-tropical dormancies that fall within the deep, programmed dormancy quadrant to be fundamentally similar.

2.2.1 | Preparation: Animals begin to accumulate energy stores while suppressing or halting reproduction

A key characteristic of programmed dormancy is that it is initiated in advance of the onset of adverse conditions. The first phase of the dormancy program is thus preparation, during which animals remodel their morphology and physiology in anticipation of dormancy proper. During the preparation phase, animals remain active with high metabolic rates and begin to store energy that will fuel metabolism during later phases. Most animals will accumulate internal lipid stores, doubling or even tripling adiposity levels (Baumgartner & Tarrant, 2017; Carey et al., 2003; Dark, 2005; Derickson, 1976; Fitzpatrick, 1976; Hahn & Denlinger, 2007; Seymour, 1973). For some small mammals (e.g. chipmunks), energy may be stored externally in food caches rather than in adipose tissue. Insects, some amphibians and fish accumulate storage proteins and carbohydrates (e.g. glycogen; Costanzo et al., 2013; Denlinger, 2002; Hahn & Denlinger, 2011; Hyvärinen et al., 1985; Vornanen et al., 2009). These glycogen stores provide crucial fuel for anaerobic metabolism in species that undergo deep, programmed dormancy in anoxic environments (i.e. crucian carp; Vornanen et al., 2009). There are hints from a range of taxa that internal lipid stores are increased through some combination of hormonally controlled hyperphagia, increased digestive efficiency and decreased energy demands (Bean et al., 1983; Dark, 2005; Florant & Healy, 2012; Schwartz et al., 2015). In addition to a general hyperphagia, preference for specific nutrients may change during preparation (Staples, 2016). For example, many mammals increase their preference for unsaturated lipids (Frank, 1994; Munro & Thomas, 2004; Staples, 2016). Some combination of dietary shifts, endogenous remodelling of nutrients and selective trafficking alters the composition of fatty acids stored internally and in the make-up of cell membranes (Arnold et al., 2011; Carey et al., 2003; Koštál, 2010; Ruf & Arnold, 2008; Seebacher, 2005).

In many animals, the suppression or halting of reproductive activity is a key part of dormancy preparation. Inhibition of reproductive physiology is often permissive for dormancy expression (i.e. reproductive hormones suppress dormancy expression; see Table 2 and **Activation**). There are exceptions to this general rule particularly in bats, echidnas and bears, where species maintain or even specifically express reproductive behaviours and activity during programmed dormancy (McAllan & Geiser, 2014). For example, several bat species are able to maintain spermatogenesis and accessory organs during dormancy (Gustafson, 1979; McAllan & Geiser, 2014; Willis, 2017), and male echidnas and bats participate in copulation during arousals from dormancy (Morrow & Nicol, 2009; Thomas et al., 1979). Female bats and echidnas may maintain pregnancy during programmed dormancy, however, gestational development is usually suspended until dormancy is complete (McAllan & Geiser, 2014; Morrow & Nicol, 2009; Nicol & Morrow, 2012; Orr & Zuk, 2013; Oxberry, 1979; Racey, 1973; Wimsatt, 1969) but see (Willis et al., 2006). In contrast, bears gestate and lactate during programmed dormancy. In the case of bears, this energetically intensive feat is associated with altered blood biochemistry and more shallow metabolic depression relative to non-reproductive individuals (Tøien et al., 2011; Wright et al., 1999).

2.2.2 | Initiation: Animals cease feeding and activity and seek a sheltered microclimate before increasing the magnitude of metabolic suppression

During initiation, animals seek microhabitats (often sheltered, but Common Poorwills and some tree-roosting bats are notable exceptions to this rule; see Turbill, 2008; Turbill & Geiser, 2008; Woods & Brigham, 2004; Woods et al., 2019) and dramatically depress or cease

TABLE 2 Conserved neuroendocrine signalling molecules involved in programmed dormancies

Conserved signalling molecules or systems	Core traits	Role	Relevant citations
Insulin signalling (mammals)/ insulin-like signalling (insects)	Metabolism, Energy storage	Signalling decreases with active metabolic suppression and increases when dormancy ends	Florant and Healy (2012), Hoehn (2004), Ragland and Keep (2017), Sim and Denlinger (2013) and Tessier et al. (2015)
Rentinoic acid receptor & Thyroid hormone (RXR/TH; vertebrates) Ultraspiracle and Juvenile hormone (USP/JH; invertebrates)	Metabolism, Energy storage	Bioavailability is gradually suppressed as animals prepare for dormancy and then increases when dormancy ends	Dardente et al. (2014) Denlinger (2002), Denlinger et al. (2011), Epperson and Martin (2002), Hut et al. (2014), Liu et al. (2017), Vermunt et al. (1999), Wheeler and Nijhout (2003) and Zhang and Denlinger (2012
Neuropeptide Y (NPY; vertebrates) Neuropeptide F (NPF; invertebrates)	Energy storage	Transition from high to low expression suppresses feeding behaviour as animals prepare to enter dormancy	Boswell et al. (1993), Huybrechts et al. (2004) and Levin et al. (2013
Ghrelin (vertebrates)	Energy Storage	Strong down-regulation associated with suppression of feeding behaviour as animals prepare to enter dormancy	Florant and Healy (2012) and Healy et al. (2010
Leptin (mammals) Unpaired 2 (Upd2; insects)	Energy Storage, Metabolism	Permissive peak associated with fattening as animals prepare to enter dormancy followed by decrease associated with metabolic suppression	Florant and Healy (2012), Freeman (2004) and Kubrak et al. (2014
Steroid hormones (Testosterone [vertebrates], Ecdysteroids [invertebrates])	Repro. activity, Metabolism?	Bioavailability may begin to increase as animals become sensitive to cues they use to end dormancy; bioavailability tends to rapidly increase when dormancy ends	Andò et al. (1992), Darrow et al. (1988), Denlinger (2002), Lee et al. (1990), Ragland et al. (2011) and Richter et al. (2016)

locomotor activity (Carey et al., 2001; Hahn & Denlinger, 2007). Energy storage has reached maximum levels by this time.

Many species cease all feeding at the onset of initiation (including one fish; Penttinen & Holopainen, 1992), and animals often dramatically decrease their digestive system volume (Cramp et al., 2009; Hahn & Denlinger, 2011; Hume et al., 2002; Martin et al., 2008; Naya et al., 2009). The gut microbiome of many animals is also modified as animals begin fasting during initiation (Bailey et al., 2010; Carey et al., 2013; Gossling et al., 1982; Liu et al., 2016; Secor & Carey, 2016; Sommer et al., 2016). For animals that consume food intermittently during dormancy, such as food-caching rodents, some bats, bears and some insect larvae (Avery, 1985; Boyles et al., 2006; Goddeeris et al., 2001; Humphries et al., 2003; Kirby et al., 2019; Krofel et al., 2016; López et al., 1995; Pigeon et al., 2016; Turbill, 2008), digestive system volume may still be reduced, but maintaining a more active gut throughout winter is likely to increase overall maintenance costs (Humphries et al., 2003).

During initiation, metabolic rate is suppressed to a fraction of active season metabolic rates, through some combination of active inhibition of metabolic pathways and passive suppression due to low temperatures (Baumgartner & Tarrant, 2017; Hahn & Denlinger, 2007; Humphries et al., 2003; Staples, 2016). In most cases, the mechanisms underlying metabolic suppression are still an open question and active field of research (Hand et al., 2011; Mathers & Staples, 2019). The cell cycle is arrested leading to a cessation of growth and development (Carey et al., 2003; Dowle et al., 2020; Hand et al., 2016).

For terrestrial ectotherms, including insects, reptiles and amphibians, body temperatures may fall below the freezing point of body tissues during dormancy in high latitude or altitude environments; thus, developing freeze tolerance or resistance is a critical process that occurs during initiation (Costanzo et al., 2013; Storey & Storey, 2013; Toxopeus & Sinclair, 2018). Endothermic hibernators defend a minimum body temperature using internal heat production when environmental temperatures fall below a critical threshold, and thus their body temperature rarely approaches freezing; however, some endotherms (e.g. arctic ground squirrels) allow their body temperature to drop as low as −2°C and thus must also employ some mechanisms (supercooling) to prevent freezing (Barnes, 1989). Stress signalling cascades may be progressively activated during the initiation phase, leading to increased levels of some protective molecules (e.g. molecular chaperones, cryoprotectants and antioxidants; Carey et al., 1999; Joanisse & Storey, 1996; King & MacRae, 2015; Lee, 2010; Moreira et al., 2016; Storey, 2010; Wijenayake et al., 2018). Although some underlying commonalities in regulation of stress hardiness may be useful to characterize dormancy, we did not feel the evidence was of sufficiently high agreement and quality to include this in the core traits at this time.

2.2.3 | Maintenance: Metabolic suppression reaches a maximum and may be interspersed with periodic arousals. Energy stores are gradually depleted

During the maintenance phase of programmed dormancy, animals exhibit deep and prolonged suppression of metabolic rate, and sustained low body temperature (provided the environment is below active season body temperature). The blood of animals including molluscs, reptiles, amphibians, and mammals becomes hypercapnic and these animals undergo respiratory acidosis (Malan, 2014). Hypercapnia may be a useful marker of dormancy progression but has not yet been investigated in a sufficiently wide range of animals to justify inclusion as a core trait.

Metabolic suppression may be punctuated by periodic arousal cycles during which metabolic rate increases and endotherms regain euthermic body temperatures (Staples, 2016). Although these arousal cycles are best known in rodent hibernators, they also occur in at least two insect species, one fish species, one lizard species and one bird species (Campbell et al., 2008; Crozier, 1979; Rismiller & McKelvey, 2000; Sláma & Denlinger, 1992; Woods et al., 2019; Figure 3). In both insects and mammals studied to-date, the period of these metabolic cycles increases to a maximum during the maintenance phase (Geiser et al., 1990; Sláma & Denlinger, 1992; Zervanos et al., 2010).

Nutrient stores are usually gradually depleted during the maintenance phase (but see Lehmann et al., 2016), and fuel preferences may shift correspondingly. Lipids are the primary fuel that animals catabolize during dormancy provided oxygen is not limiting, but proteins and carbohydrates may become more important later in dormancy, during anoxia or hypoxic periods, or under especially low environmental temperatures (Adedokun & Denlinger, 1985; Andrews, 2019; Boutilier et al., 1997; Buck & Barnes, 2000; Vornanen, 2011; Vornanen & Paajanen, 2006).

2.2.4 | Potentiation: The magnitude and recalcitrance of dormancy is gradually reduced, and animals are sensitized to the environmental cues that trigger the return to growing season physiology. Animals become competent to resume growing season activities when the environment becomes permissive

The endogenous lock put in place during initiation must be released so that animals can respond to cues that signal the return of favourable environmental conditions. Until those cues are detected, animals remain dormant, but the dormancy is now exogenously controlled. The potentiation phase includes the period over which the endogenous lock on development and activity is gradually released, until active season behaviour resumes. The mechanisms by which the endogenous lock is released is an active research area in both insect and mammal fields (Dowle et al., 2020; Hut et al., 2014; Meyers et al., 2016).

In the insect literature, this phase is currently referred to as 'termination' followed by 'post-diapause quiescence' (Koštál, 2006). In the mammalian literature, this phase has been referred to as the 'emergence period' (French, 1982), and 'termination' refers to the end of the final torpor bout or emergence from the hibernacula. We suggest '***potentiation***' as a term that could be adopted across fields and captures the gradual sensitization of the organism to cues that will trigger the resumption of activity, development, growth and (in many cases) reproduction.

The covert nature of potentiation makes this phase very difficult to detect unless manipulative experiments can be performed. In insects, this phase is diagnosed by a rapid increase in metabolic rate, or rapid development, upon return to permissive conditions (Hodek, 1996; Koštál, 2006). In mammals, torpor bout duration shortens, or mammals may experience pre-emergent euthermic intervals but retain the ability to express torpor (Geiser et al., 1990; Sláma & Denlinger, 1992; Tøien et al., 2011; Williams et al., 2014; Zervanos et al., 2010).

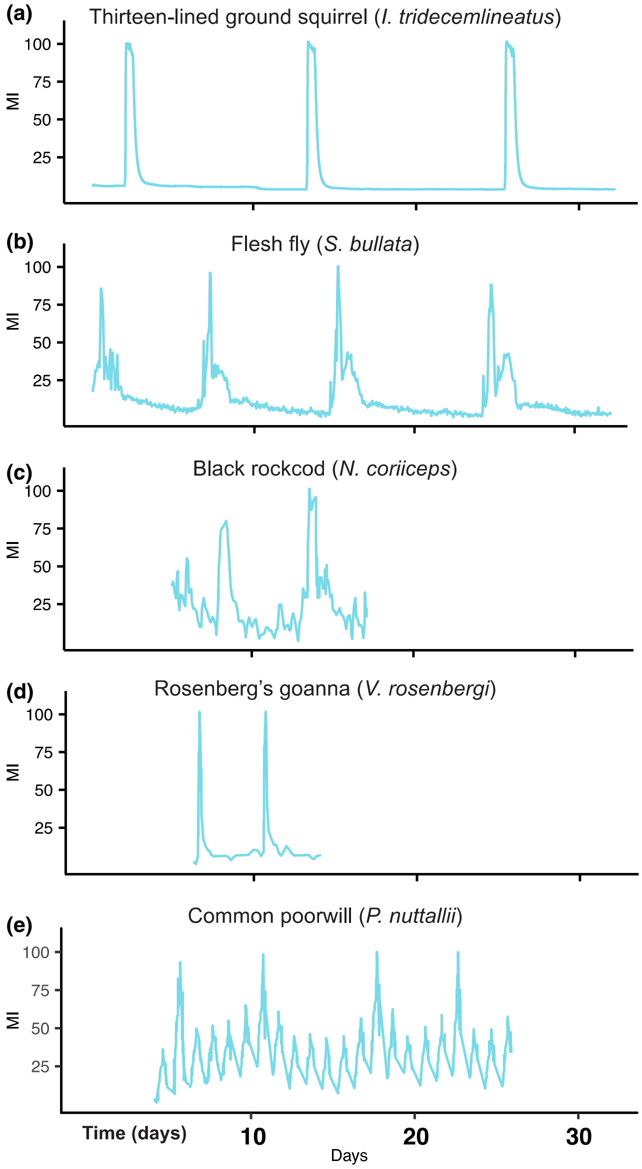

FIGURE 3 Distinctive, multi-day cycles in metabolic activity (transformed to unitless measure Metabolic Intensity (MI) for easier visual comparison, where 100 is equal to the maximum metabolic activity measured in that study) are a feature of the maintenance phase in many small mammals (a, MI represents core body temperature, unpublished data, Matthew T. Andrews), a few insect species (b, MI represents metabolic rate, unpublished data, Daniel A. Hahn and Chao Chen), at least one fish (c, MI represents heart rate, figure adapted from Campbell et al., 2008), one lizard species (d, MI represents core body temperature, figure adapted from Rismiller & McKelvey, 2000) and one bird species (e, MI represents inferred body temperature, figure adapted from Woods et al., 2019)

Potentiation may comprise a large portion of the dormant period in some species. Instances where bat species and some bears apparently become intermittently active during dormancy to feed and/or drink are consistent with an extended potentiation phase (Avery, 1985; Ben-Hamo et al., 2013; Boyles et al., 2006; Brigham, 1987; Dunbar et al., 2007; Kirby et al., 2019; Krofel et al., 2016; Lausen & Barclay, 2006; Pigeon et al., 2016; Whitaker & Rissler, 1992, 1993). Activity in bat species is often associated with more permissive environmental conditions (e.g. warmer temperatures) and may be related to an individual's dehydration status or body condition (Ben-Hamo et al., 2013; Boyles et al., 2006; Brigham, 1987; Lausen & Barclay, 2006).

The gradual decrease in dormancy recalcitrance that occurs during potentiation culminates in the animal being responsive to environmental cues that will trigger the resumption of development and activity. Thus, potentiation plays a critical role in synchronizing spring phenology of populations. The ability to respond to environmental cues is associated with increased synthesis and release of regulatory factors including many neuroendocrine hormones (Table 2) and with restored competency of target tissues (Fujiwara et al., 1995; Koštál, 2006; Koštál et al., 2017; Yamada & Mizoguchi, 2017). In some cases, the reproductive system may begin or resume development and activity, however, full competency of the reproductive axis usually requires that animals enter the activation phase (Barnes et al., 1986; McAllan & Geiser, 2014; Morrow & Nicol, 2009; Nicol & Morrow, 2012; Oxberry, 1979; Racey, 1973; Richter et al., 2016; Williams, Buck, et al., 2017; Wimsatt, 1969). Potentiation phase ends when activity and development resume, following the onset of favourable environmental conditions.

In some species or sub-groups within species (e.g. male Arctic ground squirrels), dormancy ends spontaneously without the need for external stimuli (Körtner & Geiser, 2000; Koštál, 2006; Williams, Buck, et al., 2017). In these cases, the potentiation phase does not occur.

2.2.5 | Activation: Animals resume growing season activities, rebuild tissues catabolized during dormancy, and repair accumulated damage. Activation is completed when the growing season life stage is fully realized, and physiological processes have reached full intensity

Once the appropriate cues or internal stimulus have been received, growing season processes must be restarted in a set order. In juvenile animals, growth and development must resume prior to reproductive maturation. Animals already in the adult life stage may initiate or resume reproductive activities (e.g. gestation) immediately upon entering activation.

Our fine scale understanding of the order of events during activation is limited. In insects, transcriptomic work suggests that metabolism and cellular growth/proliferation are up-regulated together before morphogenesis, growth and development; however, some of the regulatory differences leading to activation must begin in an earlier phase (i.e. during potentiation; Dowle et al., 2020; Meyers et al., 2016; Ragland et al., 2011). Similarly, we know that the same neuroendocrine systems are involved in both the inhibition and activation of reproduction in mammals as part of the dormancy program, but the connections between these systems differ between preparation/initiation and potentiation/activation (Dardente et al., 2014; Follett, 2015; Hut et al., 2014).

Feeding resumes soon after the onset of activity but may ramp up slowly (Schwartz et al., 2013). The slow onset of feeding may result in part from regrowth and remodelling of the gut (micro-villi, etc.) and the microbiome, with spring microbiotas reflecting a repopulation of an active season microbiota profile once feeding resumes (Carey et al., 2013).

The last two phases, during which animals end dormancy and return to growing season physiology, are the least understood parts of the dormancy program in all taxa.

3 | EVOLUTION AND ECOLOGY OF DORMANCY ACROSS ANIMALS

3.1 | Seasonality as a end major selective pressure underlying deep, programmed dormancy

Considering animal dormancies across the entire animal phylogeny allows us to broadly explore the association between seasonality and the major axes of dormancy. Deep, programmed dormancies such as mammalian hibernation and insect diapause are an important component of the annual cycle in seasonal environments (Carey et al., 2003; Hand et al., 2016). Seasonality can be quantified based on the predictability and magnitude of fluctuations in temperature, precipitation and primary productivity (Kreitzman & Foster, 2010; Lisovski et al., 2017; Williams, Ragland, et al., 2017). Seasonality increases with latitude, is greater in terrestrial and freshwater compared to marine habitats, and is greater in northern continental compared to southern oceanic climates (Lisovski et al., 2017; Sunday et al., 2011). Correspondingly, deep, programmed dormancy (diapause or hibernation compared to quiescence or daily torpor) is more common at high latitudes in North American mammals (Ruf & Geiser, 2015), in continental compared to oceanic climates in invertebrates (Convey, 1996; Sinclair et al., 2003), and in terrestrial and freshwater compared to marine taxa (Cáceres, 1997). The duration of dormancy increases with degree of seasonality within and among taxa (Figure 4), reflecting the longer winters at high latitudes. Exceptions to latitudinal patterns in dormancy duration occur at high altitude sites, which ecologically resemble higher latitude populations (Figure 4, dashed lines). In insects, latitudinal clines in diapause duration have been linked to genetic variation in both induction (Bradshaw & Holzapfel, 2001; Lehmann, Lyytinen, et al., 2015), and recalcitrance (Masaki, 2002; Posledovich et al., 2015). The contribution of recalcitrance to dormancy duration in other taxa has not been well documented, due to the complexity of laboratory manipulations required to isolate the factors setting dormancy duration. Dormancy magnitude, as measured by metabolic suppression, is also greater in diapausing insects from higher

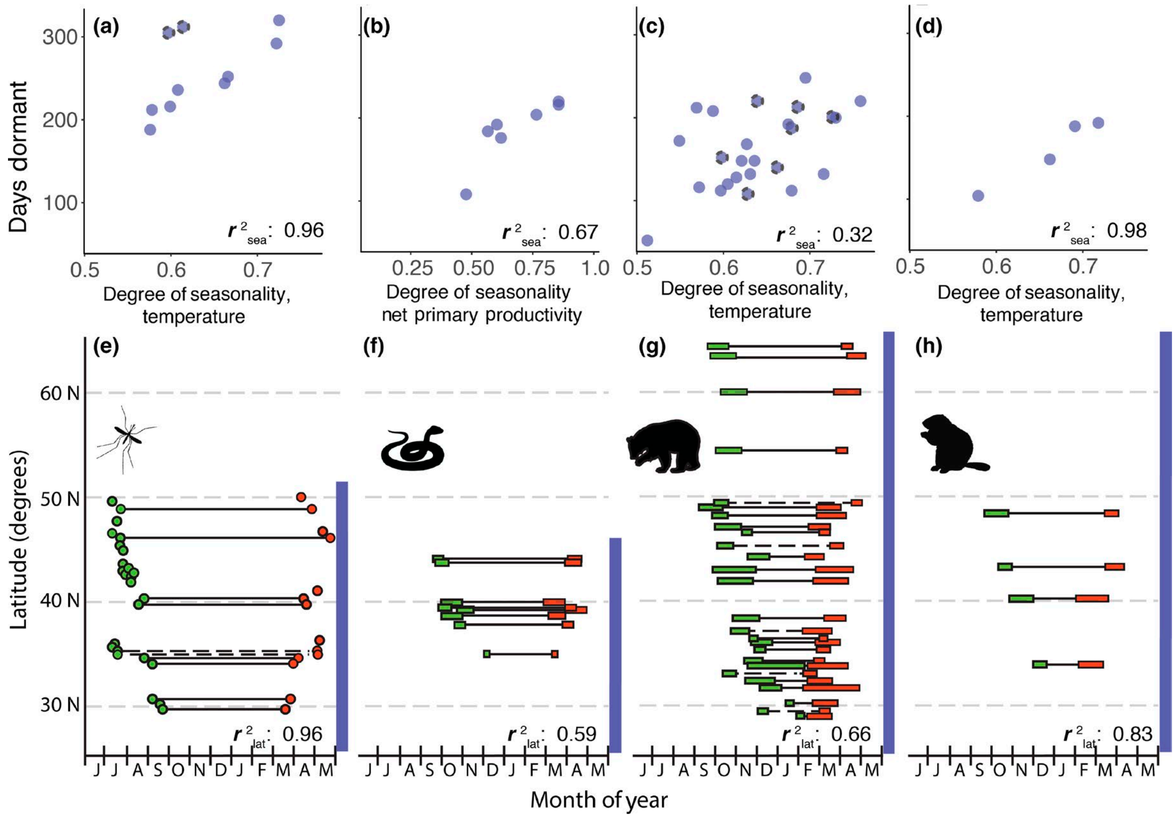

FIGURE 4 The duration of programmed dormancy across taxa is positively correlated with greater environmental seasonality. (a–d) We compiled data on dormancy duration for four North American species (a, *Wyeomyia smithii* [Pitcher plant mosquito]; b, *Elaphe obsoleta* [Ratsnake]; c, *Ursus americanus* [American black bear]; d, *Marmota monax* [Woodchuck]) and calculated dormancy duration as number of days between the earliest initiation day and latest activation day reported. Degree of seasonality temperature and primary productivity were determined using latitude and longitude from each population matched to seasonality index values from Lisovski et al., 2017 for 1 × 1 degree squares across North America (see Table S5; R^2 values from linear models including elevation as a continuous predictor are indicated in the lower right hand corner in each panel. Each blue circle corresponds to a different population; circles with dashed, black outline indicate populations resident above 500 m elevation. Results from linear models and additional details are provided in Table S6. (e–h) Because seasonality indices are highly correlated with latitude in North America (Temperature: $R^2 = 0.62$, $p < 4.9e\text{-}8$; Net primary productivity: $R^2 = 0.41$, $p < 0.002$; Precipitation: $R^2 = 0.35$, $p < 0.041$), similar patterns are evident when data are plotted by latitude (e–h, R^2 for models substituting latitude for degree of seasonality indicated in lower right of each panel). Vertical, blue bars to the right of each panel indicate species latitudinal range above 25°N. (e) Green-filled circles show critical photoperiod (CP) for diapause induction across *W. smithii* populations collected at different latitudes in North America, whereas orange-filled circles show CP for diapause termination. CPs were determined experimentally in controlled laboratory environments. Black lines connect induction and termination CPs from the same populations. CPs for both periods were not determined for all populations. Dashed lines are populations from altitudes >500 m. (f–h) Green and orange-filled bars show range or mean ± 1 *SD*, depending on data provided from each study, of dormancy initiation and activation respectively. Dashed lines show populations from altitudes >500 m

latitudes (Lehmann, Piiroinen, et al., 2015). In endotherms, the magnitude of dormancy, has not been widely assessed across populations under controlled conditions apart from the small study by Fenn et al. (2009), which is largely inconclusive because of its small sample size and confounding effects of age and sex. Diapause induction, recalcitrance and magnitude have a distinct genetic basis in insects, suggesting that they can evolve independently to match dormancy characteristics to ecological conditions (Dambroski & Feder, 2007; Masaki, 2002). An important next step is to systematically evaluate the ways that induction, recalcitrance and magnitude in multiple core traits coevolve in diverse taxa and testing whether coevolution of these traits is associated with particular aspects of seasonal environments (see Box 2).

3.2 | Origins of deep, programmed dormancy

Deep, programmed dormancy occurs broadly across the tree of life, spanning invertebrate and vertebrate lineages that split around 700 MYA (Figure 5). Extant invertebrates and vertebrates evolved from ancestors that lived in a cold and weakly seasonal ocean and the emergent groups (arthropods, molluscs and vertebrates) independently colonized more seasonal terrestrial and freshwater habitats multiple times (Lozano-Fernandez et al., 2016). The molecular machinery used to regulate the core traits involved in deep, programmed dormancy originated prior to this split. Photoperiodic sensing and daily timing is ubiquitous (Bradshaw & Holzapfel, 2007; Hut & Beersma, 2011; Kreitzman & Foster, 2010; Nelson et al., 2010), and the bases for this system

BOX 2 Key questions raised by an eco-physiological framework for animal dormancy

Ecological drivers of dormancy evolution

- Do particular aspects of seasonal environments (water and food availability, temperature, etc.) covary with the magnitude of core traits across taxa, or are the interactions between seasonal constraints and core traits taxon-specific?
- Are there predictable patterns in the relative duration of phases of the dormancy program that underlie ecologically associated phenological variation?

The physiological & molecular origins of dormancy programs

- In the diving response, some organs and regulatory processes play a critical role in facilitating longer dives, whereas others are less important (Hochachka, 2000; Hochachka & Somero, 2002). Which core traits and regulatory processes are crucial to extending dormancy duration and resistance to biochemical stressors during this period? Are these critical traits taxa-specific?
- What is the molecular basis of recalcitrance? Do clock genes play a similar role in this process across taxa?
- To what extent are molecular pathways implicated in deep, programmed dormancies involved in regulating core traits in similar ways in more responsive dormancies?
- What are the limits to maintaining suppressed metabolism for long periods? Does the existence of metabolic cycles outside of mammals indicate a shared constraint? Are the regulatory mechanisms shared or distinct?

Dormancy and life-history evolution

- Are there predictable and repeated 'adaptive walks' across dormancy axes that animals take in evolving deeper and more programmed dormancies (e.g. increases in magnitude precede increases in recalcitrance)?
- Is there a greater diversity of dormancies that exist and fall along all major axes of the dormancy program (i.e. can we 'fill out' more of the quadrants in Figure 1)? What factors constrain or facilitate the evolution of shallow, programmed dormancies across taxa?

evolved early in the tree of life (cyanobacteria; Brunner et al., 2008; Dvornyk et al., 2003; Hut & Beersma, 2011; Simons, 2009). The molecular mechanisms that coordinate metabolic arrest are also ancestral, having evolved in response to hypoxia in ancient oceans (Hochachka et al., 1993; Seebacher, 2018). However, the organization of these ancestral, component parts into a stereotypical dormancy program appears to have been repeatedly derived. Within birds and mammals, heterothermy is ancestral, but hibernation and daily torpor are seen as derived phenomena that build on this ancestral capacity (van Breukelen & Martin, 2002; Carey et al., 2003; Lovegrove, 2017; Malan, 2014; Ruf & Geiser, 2015). In insects, diapause displays rapid evolution, limited phylogenetic conservation of the diapausing life stage and apparent evolutionary convergence of gene regulation through diapause, suggesting that diapause has evolved convergently many times in many clades (Danks, 1987; Ragland & Keep, 2017; Tauber et al., 1985). The repeated co-opting and coordination of ancestral physiological systems to support derived functionality (i.e. programed dormancy) is thus analogous to the mammalian diving response, where the ancestral constituent traits are brought together in highly stereotypical ways to achieve extreme intensities and duration of a complex compound of traits (Hochachka, 2000; Hochachka & Somero, 2002). Identifying those traits that are critical for extending dormancies will be important to further defining core traits (see Box 2).

Supporting this view of repeated exaptation of ancestral building blocks, there are many examples of shared molecular mechanisms coordinating programmed dormancy, particularly in pathways that integrate environmental signals and control energy metabolism (Table 2). For example, the homologous receptors Retinoic acid receptor (*Rxr*; vertebrates) and Ultraspiracle (*Usp*; invetebrates) both appear to regulate availability of thyroid hormones (vertebrates) and juvenile hormone/ecdysteroids (invertebrates). These systems influence reproductive and metabolic amplitude across programmed dormancy, and there is evidence that they control cyclic metabolic activity during the maintenance phase (Denlinger et al., 1984; Magnus & Henderson, 1988; Schwartz et al., 2013). Insulin and insulin-like signalling pathways in mammals and insects are also regulated in similar patterns during programmed dormancy, perhaps because they converge on secondary signalling pathways that modulate cell cycle activity and metabolism (Barbieri et al., 2003; Sim & Denlinger, 2013).

3.3 | Evolutionary and life-history consequences

Animals expressing dormancy also share broader aspects of their life history. Dormancy leads to a slowing of biological time and enhanced maintenance of cellular homeostasis, including increased resistance to some types of stress (Carey et al., 2003; Hoekstra et al., 2020; Schmidt et al., 2005). Dormancy decreases mortality rates and slows senescence, leading to life span extension in both insects and mammals (Tatar et al., 2001; Tatar & Yin, 2001; Turbill et al., 2011, 2013; Turbill & Prior, 2016). Some of these life span extension effects likely arise from the thermodynamic effects of low temperatures on the rate of living (Flouris & Piantoni, 2014; Stark et al., 2018), but evidence from a range of taxa suggests that actuarial senescence is delayed due to a shut-down of neuroendocrine signalling, independent of temperature (Tatar et al., 2001; Tatar & Yin, 2001). Along with life span extension, dormancy is associated with delayed development and maturity, later age at first reproduction and reduced investment into reproduction (Schmidt et al., 2005; Tatar et al., 2001; Turbill et al., 2011). Higher diapause propensity is genetically correlated with longer life span, higher resistance to some types of stress and extended development times in *Drosophila melanogaster* (Schmidt et al., 2005), suggesting that dormancy invokes a shift towards a slower life-history

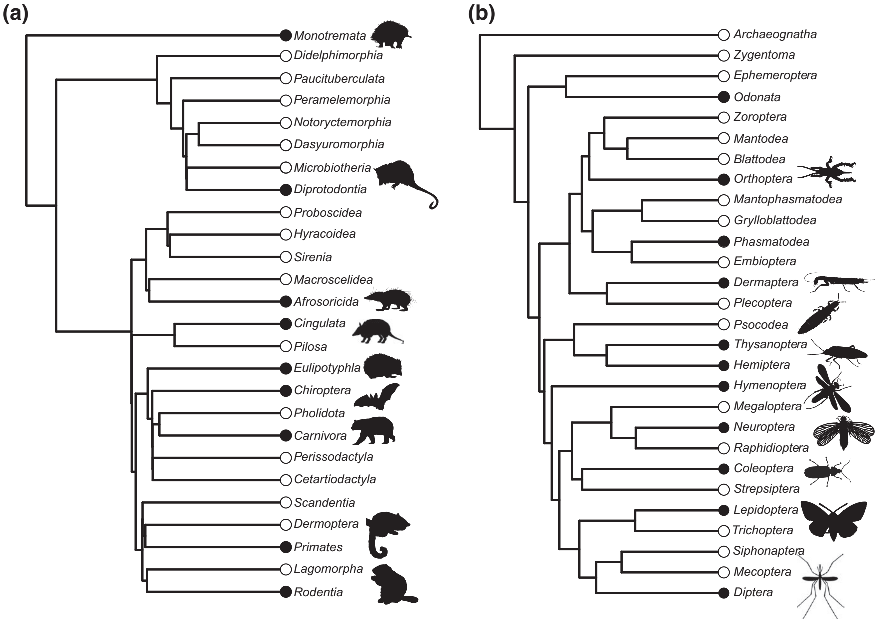

FIGURE 5 Distribution of programmed dormancy across the mammalian (a) and insect (b) phylogenies. Orders containing species that express programmed dormancy are indicated by filled circles sensu (Heldmaier et al., 2004). Most highlighted orders represent deep, programmed dormancy but a few represent shallow, programmed dormancy (e.g. Monotremata and Carnivora). See Table S6 for references. Mammal phylogeny from (Fritz et al., 2009) and insect phylogeny from (Wiens et al., 2015). Silhouettes and licenses are from phylopic.org

strategy, perhaps driven by a reallocation of resources towards somatic maintenance and away from reproduction. Our comparative framework raises questions about whether dormancy evolution and shifts in life history across taxa occur via similar processes (see Box 2). At the molecular level, this life-history shift may be facilitated by alterations to insulin signalling, a highly pleiotropic pathway which regulates growth, energy metabolism and life span, and is involved in dormancy regulation in a wide range of taxa (see Table 2; McGaugh et al., 2015; Sim & Denlinger, 2008; Sparkman et al., 2012; Williams et al., 2006; Wolkow et al., 2000).

4 | OPPORTUNITIES AND OUTLOOK

Our framework uses three main components (axes, phases and core traits) to categorize and quantifying ecologically relevant variation in dormancies across animal taxa. The axes (induction, recalcitrance and magnitude) provide an experimentally tractable means of categorizing dormancy that can be compared among species across the animal phylogeny, and they capture the ecologically relevant aspects of dormancy more richly than traditional dichotomies such as diapause/quiescence or hibernation/daily torpor. Induction and recalcitrance are ecologically important because they together determine the length of dormancy, and their underlying physiological and molecular mechanisms are the material that evolution acts on to fine-tune dormancy duration to environmental conditions. The magnitude of dormancy is ecologically important because it determines strategies of energy acquisition (e.g. requirements for energy storage during preparation, locomotor performance during dormancy setting ability to forage) and allocation (e.g. maintenance costs during dormancy, setting rates of energy depletion). Using these three axes allows us to clearly separate the shallow reproductive diapause of *Drosophila melanogaster* from the deep programmed diapause of *Sarcophaga bullata*, and to differentiate between an annual aestivation seen in *Cheirogaleus medius* and the more responsive aestivation displayed by *Glis glis*.

The phases allow us to compare experimental data according to biological rather than calendar time, and, by using diagnostic traits that occur across taxa, open up opportunities for comparative research. Applying these phases to a mammalian hibernator suggests that the relative length of phases differs along a latitudinal gradient (Figure 6), suggesting that increased duration of dormancy does not simply reflect extension of a single phase (e.g. maintenance). While we do not expect researchers to abandon field-specific terminology, signposting phases in which experimental data are collected using this framework will facilitate an integration of fields in the primary literature, addressing the extreme siloing that we documented in our literature search.

The core traits are useful because they can provide a multi-faceted quantitation of the degree of intra- and interspecific variation in dormancy magnitude and regulation. For this benefit to be realized, we need a standardized way of measuring the degree of plasticity in each trait. We suggest that, for comparative purposes, researchers report the maximum change in core traits relative to specified active season values (e.g. reproductive or non-reproductive). Defining degree of suppression is already common in the case of metabolic rate, allowing us to compare the degree of metabolic suppression of poikilotherms and mammals (e.g. Guppy & Withers, 1999; Ruf & Geiser, 2015), and extending this approach can be used to quantify the degree of energy accumulation and depletion and the degree of reduction in locomotor and reproductive activity. Conceptualizing these core traits as components of the dormancy program that can be tweaked independently suggests core molecular and metabolic pathways that may be altered in animals expressing similar dormancy types.

A unification of fields of dormancy research offers broad opportunities for cross-pollination of research questions and hypotheses. For example, in the insect literature, clines in clock gene allele frequency underlie evolved differences in diapause induction and initiation timing, and these alleles are under selection due to climate change (Bradshaw & Holzapfel, 2001;

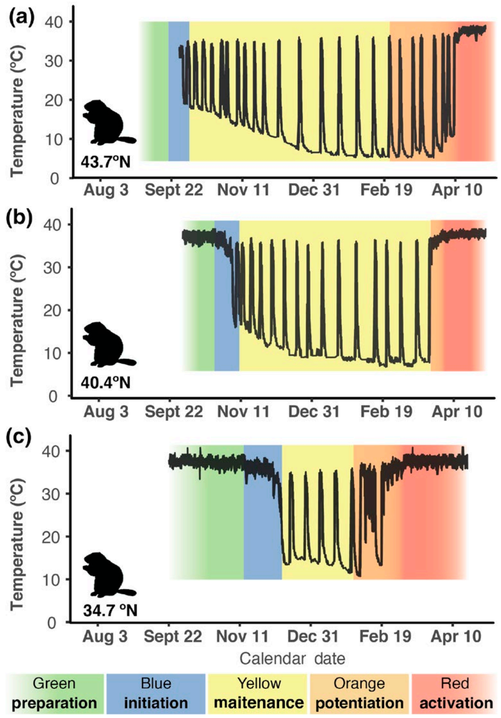

FIGURE 6 Qualitatively delineated phases in the dormancy program may not vary proportionally in duration with dormancy period across latitudes or by species. (a–c) Body temperature traces from hibernating Woodchucks (*Marmota monax*, data from S. Zervanos). Body temperature traces from each population were qualitatively divided into phases of dormancy (Green, Preparation; Blue, Initiation; Yellow, Maintenance; Orange, Potentiation; Red, Activation). Duration of each phase can vary among individuals and populations, and it will vary inter-annually within populations

Pruisscher et al., 2018). Similar clines in timing also exist in other taxa (Figures 4 and 6), but we do not know the extent to which they share a common mechanism (see Box 2; Fenn et al., 2009; Grabek et al., 2019; Lane et al., 2011, 2019; Zervanos et al., 2010). The mammalian literature has shown that diet during preparation may influence the magnitude and duration of maintenance phase. Does diet meaningfully influence programmed dormancy in insects and other animals that have a greater ability to modify lipids endogenously? Other interesting avenues include the role of sex steroids in phenology (e.g. protandry) outside of ground squirrels (Richter et al., 2016; Williams, Buck, et al., 2017), the prevalence of hypercapnia and respiratory acidosis in insects (Malan, 2014) and common mechanisms by which dormancy recalcitrance is reduced during maintenance and potentiation phases (Dowle et al., 2020; Hut et al., 2014; Koštál, 2006; Meyers et al., 2016; Powell et al., 2020; Wadsworth et al., 2013).

Inevitably, creating a broad and generalizable framework requires glossing over some exceptions and system-specific details. Some of the physiological and ecological processes that are discussed here as analogous across species will not appear so as we learn more, researchers working on animals outside the insect and mammal systems that we have focused on will no doubt have insights that will require the framework to adapt and expand. Broad application of the framework will require substantial conceptual and experimental work from researchers across fields. However, we hope that the framework outlined here will provide a starting point for that work to take place. We strongly believe that a broad and phylogenetically inclusive dormancy framework will facilitate a better understanding of both the mechanisms and origins of dormancy, stimulating forward momentum and novel directions for the broader field of dormancy research.

ACKNOWLEDGEMENTS

We are grateful to B. M. Barnes, D. I. Bolnick, H. V. Carey, D. A. Hahn, R. B. Huey, V. Koštál, J.-F. Lemaître, M. D. Regan, C. T. Williams and six anonymous reviewers for generously providing feedback on previous drafts of this manuscript. L. Ferguson, S. Finnegan, L. Hlusko, D. Levesque, B. Sinclair, P. Sudmant and J.-P. Vázquez-Medina, gave invaluable feedback and ideas on parts of the framework. While this truly was a team effort in many ways, all errors in the final manuscript are ours. C. Chen, D. A. Hahn, M. T. Andrews, G. Florant, S. M. Zervanos and C. Woods kindly provided data for the manuscript.

AUTHORS' CONTRIBUTIONS

All authors contributed equally to developing the ideas and writing the manuscript.

DATA AVAILABILITY STATEMENT

There are no data to archive for this manuscript.

ORCID

Kathryn Wilsterman https://orcid.org/0000-0001-7262-9754
Mallory A. Ballinger https://orcid.org/0000-0003-3087-0608
Caroline M. Williams https://orcid.org/0000-0003-3112-0286

REFERENCES

Adedokun, T. A., & Denlinger, D. L. (1985). Metabolic reserves associated with pupal diapause in the flesh fly, *Sarcophaga crassipalpis*. *Journal of Insect Physiology*, *31*, 229–233. https://doi.org/10.1016/0022-1910(85)90124-6

Andò, S., Ciarcia, G., Panno, M. L., Imbrogno, E., Tarantino, G., Buffone, M., Beraldi, E., Angelini, F., & Botte, V. (1992). Sex steroids levels in the plasma and testis during the reproductive cycle of lizard *Podarcis s. sicula* raf. *General and Comparative Endocrinology*, *85*, 1–7. https://doi.org/10.1016/0016-6480(92)90165-G

Andrewartha, H. G. (1952). Diapause in relation to the ecology of insects. *Biological Reviews*, *27*, 50–107. https://doi.org/10.1111/j.1469-185X.1952.tb01363.x

Andrews, M. T. (2019). Molecular interactions underpinning the phenotype of hibernation in mammals. *Journal of Experimental Biology*, *222*(2), jeb160606. https://doi.org/10.1242/jeb.160606

Arnold, W. (2020). Review: Seasonal differences in the physiology of wild northern ruminants. *Animal: an International Journal of Animal BioScience*, *14*, s124–s132. https://doi.org/10.1017/S1751731119003240

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

Avery, M. I. (1985). Winter activity of pipistrelle bats. *Journal of Animal Ecology*, *54*, 721–738. https://doi.org/10.2307/4374

Bailey, M. T., Walton, J. C., Dowd, S. E., Weil, Z. M., & Nelson, R. J. (2010). Photoperiod modulates gut bacteria composition in male Siberian hamsters (*Phodopus sungorus*). *Brain, Behavior, and Immunity*, *24*, 577–584. https://doi.org/10.1016/j.bbi.2009.12.010

Barbieri, M., Bonafè, M., Franceschi, C., & Paolisso, G. (2003). Insulin/IGF-I-signaling pathway: An evolutionarily conserved mechanism of longevity from yeast to humans. *American Journal of Physiology-Endocrinology and Metabolism*, *285*, E1064–E1071. https://doi.org/10.1152/ajpendo.00296.2003

Barnes, B. M. (1989). Freeze avoidance in a mammal: Body temperatures below 0°C in an arctic hibernator. *Science*, *244*, 1593–1595.

Barnes, B. M., Kretzmann, M., Licht, P., & Zucker, I. (1986). The influence of hibernation on testis growth and spermatogenesis in the golden-mantled ground squirrel, *Spermophilus lateralis*. *Biology of Reproduction*, *35*, 1289–1297.

Baumgartner, M. F., & Tarrant, A. M. (2017). The physiology and ecology of diapause in marine copepods. *Annual Review of Marine Science*, *9*, 387–411. https://doi.org/10.1146/annurev-marine-010816-060505

Bean, D. W., Goodman, W. G., & Beck, S. D. (1983). Regulation of juvenile hormone esterase activity in the European corn borer, *Ostrinia nubilalis*. *Journal of Insect Physiology*, *29*, 877–883. https://doi.org/10.1016/0022-1910(83)90050-1

Ben-Hamo, M., Muñoz-Garcia, A., Williams, J. B., Korine, C., & Pinshow, B. (2013). Waking to drink: Rates of evaporative water loss determine arousal frequency in hibernating bats. *Journal of Experimental Biology*, *216*, 573–577. https://doi.org/10.1242/jeb.078790

Bieber, C., & Ruf, T. (2009). Summer dormancy in edible dormice (*Glis glis*) without energetic constraints. *Die Naturwissenschaften*, *96*, 165–171. https://doi.org/10.1007/s00114-008-0471-z

Borzée, A., Choi, Y., Kim, Y. E., Jablonski, P. G., & Jang, Y. (2019). Interspecific variation in seasonal migration and brumation behavior in two closely related species of treefrogs. *Frontiers in Ecology and Evolution*, *7*, 55. https://doi.org/10.3389/fevo.2019.00055

Boswell, T., Richardson, R. D., Schwartz, M. W., D'Alessio, D. A., Woods, S. C., Sipols, A. J., Baskin, D. G., & Kenagy, G. J. (1993). NPY and galanin in a hibernator: Hypothalamic gene expression and effects on feeding. *Brain Research Bulletin*, *32*, 379–384. https://doi.org/10.1016/0361-9230(93)90203-N

Boutilier, R. G., Donohoe, P. H., Tattersall, G. J., & West, T. G. (1997). Hypometabolic homeostasis in overwintering aquatic amphibians. *Journal of Experimental Biology*, *200*, 387–400.

Boyles, J. G., Dunbar, M. B., & Whitaker, J. O. (2006). Activity following arousal in winter in North American vespertilionid bats. *Mammal Review*, *36*, 267–280. https://doi.org/10.1111/j.1365-2907.2006.00095.x

Bradshaw, W. E., & Holzapfel, C. M. (2001). Genetic shift in photoperiodic response correlated with global warming. *Proceedings of the National Academy of Sciences of the United States of America*, *98*, 14509–14511. https://doi.org/10.1073/pnas.241391498

Bradshaw, W. E., & Holzapfel, C. M. (2007). Evolution of animal photoperiodism. *Annual Review of Ecology, Evolution, and Systematics*, *38*, 1–25. https://doi.org/10.1146/annurev.ecolsys.37.091305.110115

Brigham, R. M. (1987). The significance of winter activity by the big brown bat (*Eptesicus fuscus*): The influence of energy reserves. *Canadian Journal of Zoology*, *65*, 1240–1242.

Brunner, M., Simons, M. J. P., & Merrow, M. (2008). Lego clocks: Building a clock from parts. *Genes & Development*, *22*, 1422–1426. https://doi.org/10.1101/gad.1686608

Buck, C. L., & Barnes, B. M. (2000). Effects of ambient temperature on metabolic rate, respiratory quotient, and torpor in an arctic hibernator. *American Journal of Physiology: Regulatory, Integrative and Comparative Physiology*, *279*, R255–262.

Cáceres, C. E. (1997). Dormancy in invertebrates. *Invertebrate Biology*, *116*, 371–383. https://doi.org/10.2307/3226870

Campbell, H. A., Fraser, K. P. P., Bishop, C. M., Peck, L. S., & Egginton, S. (2008). Hibernation in an antarctic fish: On ice for winter. *PLoS ONE*, *3*, e1743. https://doi.org/10.1371/journal.pone.0001743

Carey, H. V., Andrews, M. T., & Martin, S. L. (2003). Mammalian hibernation: Cellular and molecular responses to depressed metabolism and low temperature. *Physiological Reviews*, *83*, 1153–1181. https://doi.org/10.1152/physrev.00008.2003

Carey, H. V., Mangino, M. J., & Southard, J. H. (2001). Changes in gut function during hibernation: Implications for bowel transplantation and surgery. *Gut*, *49*, 459–461. https://doi.org/10.1136/gut.49.4.459

Carey, H. V., Sills, N. S., & Gorham, D. A. (1999). Stress proteins in mammalian hibernation. *Integrative and Comparative Biology*, *39*, 825–835.

Carey, H. V., Walters, W. A., & Knight, R. (2013). Seasonal restructuring of the ground squirrel gut microbiota over the annual hibernation cycle. *AJP: Regulatory, Integrative and Comparative Physiology*, *304*, R33–R42.

Convey, P. (1996). Overwintering strategies of terrestrial invertebrates in Antarctica – The significance of flexibility in extremely seasonal environments. *EJE*, *93*, 489–505.

Costanzo, J. P., do Amaral, M. C. F., Rosendale, A. J., & Lee, R. E. (2013). Hibernation physiology, freezing adaptation and extreme freeze tolerance in a northern population of the wood frog. *Journal of Experimental Biology*, *216*, 3461–3473. https://doi.org/10.1242/jeb.089342

Cramp, R. L., Kayes, S. M., Meyer, E. A., & Franklin, C. E. (2009). Ups and downs of intestinal function with prolonged fasting during aestivation in the burrowing frog, *Cyclorana alboguttata*. *Journal of Experimental Biology*, *212*, 3656–3663. https://doi.org/10.1242/jeb.027748

Crozier, A. J. G. (1979). Supradian and infradian cycles in oxygen uptake of diapausing pupae of *Pieris brassicae*. *Journal of Insect Physiology*, *25*, 575–582. https://doi.org/10.1016/0022-1910(79)90072-6

Dambroski, H. R., & Feder, J. L. (2007). Host plant and latitude-related diapause variation in *Rhagoletis pomonella*: A test for multifaceted life history adaptation on different stages of diapause development. *Journal of Evolutionary Biology*, *20*, 2101–2112. https://doi.org/10.1111/j.1420-9101.2007.01435.x

Danks, H. V. (1987). *Insect dormancy: An ecological perspective* (Vol. 1). Biological Survey of Canada (Terrestrial Artropods).

Dardente, H., Hazlerigg, D. G., & Ebling, F. J. P. (2014). Thyroid hormone and seasonal rhythmicity. *Frontiers in Endocrinology*, *5*, 19. https://doi.org/10.3389/fendo.2014.00019

Dark, J. (2005). Annueal lipids cycles in hibernators: Integration of physiology and behavior. *Annual Review of Nutrition*, *25*, 469–497.

Darrow, J. M., Duncan, M. J., Bartke, A., Bona-Gallo, A., & Goldman, B. D. (1988). Influence of photoperiod and gonadal steroids on hibernation in the European hamster. *Journal of Comparative Physiology A*, *163*, 339–348. https://doi.org/10.1007/BF00604009

Dausmann, K. H., Glos, J., Ganzhorn, J. U., & Heldmaier, G. (2004). Hibernation in a tropical primate. *Nature*, *429*, 825–826. https://doi.org/10.1038/429825a

Denlinger, D. L. (1972). Induction and termination of pupal diapause in sarcophaga (Diptera: Sarcophagidae). *Biological Bulletin*, *142*, 11–24.

Denlinger, D. L. (2002). Regulation of diapause. *Annual Review of Entomology*, *47*, 93–122. https://doi.org/10.1146/annurev.ento.47.091201.145137

Denlinger, D. L., Shukla, M., & Faustini, D. L. (1984). Juvenile hormone involvement in pupal diapause of the flesh fly *Sarcophaga crassipalpis*: Regulation of infradian cycles of O_2 consumption. *Journal of Experimental Biology*, *109*, 191–199.

Denlinger, D. L., Yocum, G., & Rinehart, J. P. (2011). Hormonal control of diapause. In L. I. Gilbert (Ed.), *Insect endocrinology* (pp. 430–463). Academic Press.

Derickson, W. K. (1976). Lipid storage and utilization in reptiles. *American Zoologist*, *16*, 711–723. https://doi.org/10.1093/icb/16.4.711

Dowle, E. J., Powell, T. H. Q., Doellman, M. M., Meyers, P. J., Calvert, M. C. B., Walden, K. K. O., Robertson, H. M., Berlocher, S. H., Feder, J. L., Hahn, D. A., & Ragland, G. J. (2020). Genome-wide variation and transcriptional changes in diverse developmental processes underlie the rapid evolution of seasonal adaptation. *Proceedings of the National Academy of Sciences of the United States of America*, *117*, 23960–23969. https://doi.org/10.1073/pnas.2002357117

Duerr, J. M., & Podrabsky, J. E. (2010). Mitochondrial physiology of diapausing and developing embryos of the annual killifish *Austrofundulus limnaeus*: Implications for extreme anoxia tolerance. *Journal of Comparative Physiology B*, *180*, 991–1003. https://doi.org/10.1007/s00360-010-0478-6

Dunbar, M. B., Whitaker Jr., J. O., & Robbins, L. W. (2007). Winter feeding by bats in Missouri. *Acta Chiropterologica*, *9*, 305–310.

Dvornyk, V., Vinogradova, O., & Nevo, E. (2003). Origin and evolution of circadian clock genes in prokaryotes. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 2495–2500. https://doi.org/10.1073/pnas.0130099100

Epperson, L. E., & Martin, S. L. (2002). Quantitative assessment of ground squirrel mRNA levels in multiple stages of hibernation. *Physiological Genomics*, *10*, 93–102. https://doi.org/10.1152/physiolgenomics.00004.2002

Faherty, S. L., Villanueva-Cañas, J. L., Blanco, M. B., Albà, M. M., & Yoder, A. D. (2018). Transcriptomics in the wild: Hibernation physiology in free-ranging dwarf lemurs. *Molecular Ecology*, *27*, 709–722. https://doi.org/10.1111/mec.14483

Fenn, A. M., Zervanos, S. M., & Florant, G. L. (2009). Energetic relationships between field and laboratory woodchucks (*Marmota monax*) along a latitudinal gradient. *Ethology Ecology & Evolution*, *21*, 299–315.

Fietz, J., & Dausmann, K. H. (2007). Big is beautiful: fat storage and hibernation as a strategy to cope with marked seasonality in the fat-tailed Dwarf Lemur (*Cheirogaleus medius*). In L. Gould & M. L. Sauther (Eds.), *Lemurs: Ecology and adaptation, developments in primatology: Progress and prospect* (pp. 97–110). Springer.

Fitzpatrick, L. C. (1976). Life history patterns of storage and utilization of lipids for energy in amphibians. *Integrative and Comparative Biology*, *16*, 725–732.

Florant, G. L., & Healy, J. E. (2012). The regulation of food intake in mammalian hibernators: A review. *Journal of Comparative Physiology B*, *182*, 451–467. https://doi.org/10.1007/s00360-011-0630-y

Flouris, A. D., & Piantoni, C. (2014). Links between thermoregulation and aging in endotherms and ectotherms. *Temperature: Multidisciplinary Biomedical Journal*, *2*, 73–85. https://doi.org/10.4161/23328940.2014.989793

Follett, B. K. (2015). 'Seasonal changes in the neuroendocrine system': Some reflections. *Frontiers in Neuroendocrinology*, *37*, 3–12. https://doi.org/10.1016/j.yfrne.2014.11.003

Frank, C. L. (1994). Polyunsaturate content and diet selection by ground squirrels (*Spermophilus Lateralis*). *Ecology*, *75*, 458–463. https://doi.org/10.2307/1939549

Freeman, D. A. (2004). Reduced leptin concentrations are permissive for display of torpor in Siberian hamsters. *AJP: Regulatory, Integrative and Comparative Physiology*, *287*, R97–R103.

French, A. R. (1982). Intraspecific differences in the pattern of hibernation in the ground squirrel *Spermophilus beldingi*. *Journal of Comparative Physiology*, *148*, 83–91. https://doi.org/10.1007/BF00688891

Fritz, S. A., Bininda-Emonds, O. R. P., & Purvis, A. (2009). Geographical variation in predictors of mammalian extinction risk: Big is bad, but only in the tropics. *Ecology Letters*, *12*, 538–549. https://doi.org/10.1111/j.1461-0248.2009.01307.x

Fujiwara, H., Jindra, M., Newitt, R., Palli, S. R., Hiruma, K., & Riddiford, L. M. (1995). Cloning of an ecdysone receptor homolog from *Manduca sexta* and the developmental profile of its mRNA in wings. *Insect Biochemistry and Molecular Biology*, *25*, 845–856. https://doi.org/10.1016/0965-1748(95)00023-O

Gatten, R. E. (1978). Aerobic metabolism in snapping turtles, *Chelydra serpentina*, after thermal acclimation. *Comparative Biochemistry and Physiology Part A: Physiology*, *61*, 325–337. https://doi.org/10.1016/0300-9629(78)90116-0

Geiser, F. (1998). Evolution of daily torpor and hibernation in birds and mammals: Importance of body size. *Clinical and Experimental Pharmacology and Physiology*, *25*, 736–740. https://doi.org/10.1111/j.1440-1681.1998.tb02287.x

Geiser, F. (2010). Aestivation in mammals and birds. In C. Arturo Navas & J. E. Carvalho (Eds.), *Aestivation: Molecular and physiological aspects, progress in molecular and subcellular biology* (pp. 95–111). Springer.

Geiser, F. (2013). Hibernation. *Current Biology*, *23*, R188–R193. https://doi.org/10.1016/j.cub.2013.01.062

Geiser, F. (2020). Seasonal expression of avian and mammalian daily torpor and hibernation: Not a simple summer-winter affair†. *Frontiers in Physiology*, *11*, 436. https://doi.org/10.3389/fphys.2020.00436

Geiser, F., Hiebert, S., & Kenagy, G. J. (1990). Torpor bout duration during the hibernation season of two sciurid rodents: Interrelations with temperature and metabolism. *Physiological Zoology*, *63*, 489–503. https://doi.org/10.1086/physzool.63.3.30156224

Goddeeris, B., Vermeulen, A. C., de Geest, E., Jacobs, H., Baert, B., & Ollevier, F. (2001). Diapause induction in the third and fourth instar of *Chironomus riparius* (Diptera) from Belgian lowland brooks. *Archiv Für Hydrobiologie*, *150*(2), 307–327. https://doi.org/10.1127/archiv-hydrobiol/150/2001/307

Gossling, J., Loesche, W. J., & Nace, G. W. (1982). Large intestine bacterial flora of nonhibernating and hibernating leopard frogs (*Rana pipiens*). *Applied and Environmental Microbiology*, *44*, 59–66. https://doi.org/10.1128/AEM.44.1.59-66.1982

Grabek, K. R., Cooke, T. F., Epperson, L. E., Spees, K. K., Cabral, G. F., Sutton, S. C., Merriman, D. K., Martin, S. L., & Bustamante, C. D. (2019). Genetic variation drives seasonal onset of hibernation in the 13-lined ground squirrel. *Communications Biology*, *2*, 1–13. https://doi.org/10.1038/s42003-019-0719-5

Guppy, M., & Withers, P. (1999). Metabolic depression in animals: Physiological perspectives and biochemical generalizations. *Biological Reviews*, *74*, 1–40. https://doi.org/10.1017/S0006323198005258

Gustafson, A. W. (1979). Male reproductive patterns in hibernating bats. *Reproduction*, *56*, 317–331. https://doi.org/10.1530/jrf.0.0560317

Hahn, D. A., & Denlinger, D. L. (2007). Meeting the energetic demands of insect diapause: Nutrient storage and utilization. *Journal of Insect Physiology*, *53*, 760–773. https://doi.org/10.1016/j.jinsphys.2007.03.018

Hahn, D. A., & Denlinger, D. L. (2011). Energetics of insect diapause. *Annual Review of Entomology*, *56*, 103–121. https://doi.org/10.1146/annurev-ento-112408-085436

Hand, S. C. (1991). Metabolic dormancy in aquatic invertebrates. In M. A. Castellini, B. Fiévet, S. C. Hand, R. Motais, B. Pelster, & R. E. Weber (Eds.), *Advances in comparative and environmental physiology, Volume 8, Advances in comparative and environmental physiology* (pp. 1–50). Springer Berlin Heidelberg.

Hand, S. C., Denlinger, D. L., Podrabsky, J. E., & Roy, R. (2016). Mechanisms of animal diapause: Recent developments from nematodes, crustaceans, insects, and fish. *American Journal of Physiology – Regulatory, Integrative and Comparative Physiology*, *310*, R1193–R1211.

Hand, S. C., Menze, M. A., Borcar, A., Patil, Y., Covi, J. A., Reynolds, J. A., & Toner, M. (2011). Metabolic restructuring during energy-limited states: Insights from *Artemia franciscana* embryos and other animals. *Journal of Insect Physiology*, *57*, 584–594. https://doi.org/10.1016/j.jinsphys.2011.02.010

Harlow, H. J., & Menkens Jr., G. E. (1986). A comparison of hibernation in the black-tailed prairie dog, white-tailed prairie dog, and Wyoming ground squirrel. *Canadian Journal of Zoology*, *64*, 793–796. https://doi.org/10.1139/z86-118

Healy, J. E., Ostrom, C. E., Wilkerson, G. K., & Florant, G. L. (2010). Plasma ghrelin concentrations change with physiological state in a sciurid hibernator (*Spermophilus lateralis*). *General and Comparative Endocrinology*, *166*, 372–378. https://doi.org/10.1016/j.ygcen.2009.12.006

Heldmaier, G., Ortmann, S., & Elvert, R. (2004). Natural hypometabolism during hibernation and daily torpor in mammals. *Respiratory Physiology & Neurobiology*, *Hypoxic Hypometabolism*, *141*, 317–329. https://doi.org/10.1016/j.resp.2004.03.014

Hirche, H.-J. (1996). Diapause in the marine copepod, *Calanus finmarchicus*—A review. *Ophelia*, *44*, 129–143.

Hochachka, P. W. (2000). Pinniped diving response mechanism and evolution: A window on the paradigm of comparative biochemistry and physiology. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *126*, 435–458. https://doi.org/10.1016/S1095-6433(00)00231-2

Hochachka, P. W., Lutz, P. L., Sick, T. J., & Rosenthal, M. (1993). *Surviving hypoxia: Mechanisms of control and adaptation*. CRC Press.

Hochachka, P. W., & Somero, G. N. (2002). *Biochemical adaptation: Mechanism and process in physiological evolution*. Oxford University Press.

Hodek, I. (1996). Diapause development, diapause termination and the end of diapause. *EJE*, *93*, 475–487.

Hodek, I. (2002). Controversial aspects of diapause development. *European Journal of Entomology*, *99*, 163–173. https://doi.org/10.14411/eje.2002.024

Hoehn, K. L. (2004). Seasonal, tissue-specific regulation of Akt/protein kinase B and glycogen synthase in hibernators. *AJP: Regulatory. Integrative and Comparative Physiology*, *286*, 498R–504.

Hoekstra, L. A., Schwartz, T. S., Sparkman, A. M., Miller, D. A. W., & Bronikowski, A. M. (2020). The untapped potential of reptile biodiversity for understanding how and why animals age. *Functional Ecology*, *34*, 38–54. https://doi.org/10.1111/1365-2435.13450

Hoelzl, F., Bieber, C., Cornils, J. S., Gerritsmann, H., Stalder, G. L., Walzer, C., & Ruf, T. (2015). How to spend the summer? Free-living dormice (*Glis glis*) can hibernate for 11 months in non-reproductive years. *Journal of Comparative Physiology. B*, *Biochemical*, *Systemic*, *and Environmental Physiology*, *185*, 931–939. https://doi.org/10.1007/s00360-015-0929-1

Hume, D., Beiglböck, C., Ruf, T., Frey-Roos, F., Bruns, U., & Arnold, W. (2002). Seasonal changes in morphology and function of the gastrointestinal tract of free-living alpine marmots (*Marmota marmota*). *Journal of Comparative Physiology. B*, *Biochemical*, *Systemic*, *and Environmental Physiology*, *172*, 197–207. https://doi.org/10.1007/s00360-001-0240-1

Humphries, M. M., Thomas, D. W., & Kramer, D. L. (2003). The role of energy availability in mammalian hibernation: A cost-benefit approach. *Physiological and Biochemical Zoology*, *76*, 165–179. https://doi.org/10.1086/367950

Hut, R. A., & Beersma, D. G. M. (2011). Evolution of time-keeping mechanisms: Early emergence and adaptation to photoperiod. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 2141–2154. https://doi.org/10.1098/rstb.2010.0409

Hut, R. A., Dardente, H., & Riede, S. J. (2014). Seasonal timing: How does a hibernator know when to stop hibernating? *Current Biology*, *24*, R602–R605. https://doi.org/10.1016/j.cub.2014.05.061

Huybrechts, J., De Loof, A., & Schoofs, L. (2004). Diapausing Colorado potato beetles are devoid of short neuropeptide F I and II. *Biochemical and Biophysical Research Communications*, *317*, 909–916. https://doi.org/10.1016/j.bbrc.2004.03.136

Hyvärinen, H., Holopainen, I. J., & Piironen, J. (1985). Anaerobic wintering of crucian carp (*Carassius carassius* L.)-I. Annual dynamics of glycogen reserves in nature. *Comparative Biochemistry and Physiology Part A: Physiology*, *82*, 797–803.

Joanisse, D. R., & Storey, K. B. (1996). Oxidative damage and antioxidants in *Rana sylvatica*, the freeze-tolerant wood frog. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, *271*, R545–R553.

Jönsson, K. I., Holm, I., & Tassidis, H. (2019). Cell biology of the Tardigrades: Current knowledge and perspectives. In W. Tworzydlo & S. M. Bilinski (Eds.), *Evo-devo: Non-model species in cell and developmental biology*, *results and problems in cell differentiation* (pp. 231–249). Springer International Publishing.

King, A. M., & MacRae, T. H. (2015). Insect heat shock proteins during stress and diapause. *Annual Review of Entomology*, *60*, 59–75. https://doi.org/10.1146/annurev-ento-011613-162107

Kirby, R., Johnson, H. E., Alldredge, M. W., & Pauli, J. N. (2019). The cascading effects of human food on hibernation and cellular aging in free-ranging black bears. *Scientific Reports*, *9*, 2197. https://doi.org/10.1038/s41598-019-38937-5

Körtner, G., & Geiser, F. (2000). The temporal organization of daily torpor and hibernation: Circadian and circannual rhythms. *Chronobiology International*, *17*, 103–128. https://doi.org/10.1081/CBI-100101036

Koštál, V. (2006). Eco-physiological phases of insect diapause. *Journal of Insect Physiology*, *52*, 113–127. https://doi.org/10.1016/j.jinsphys.2005.09.008

Koštál, V. (2010). Cell structural modifications in insects at low temperatures. In D. L. Denlinger & R. E. Lee Jr (Eds.), *Low temperature biology of insects* (pp. 116–140). Cambridge University Press.

Koštál, V., Shimada, K., & Hayakawa, Y. (2000). Induction and development of winter larval diapause in a drosophilid fly, *Chymomyza costata*. *Journal of Insect Physiology*, *46*, 417–428. https://doi.org/10.1016/S0022-1910(99)00124-9

Koštál, V., Štětina, T., Poupardin, R., Korbelová, J., & Bruce, A. W. (2017). Conceptual framework of the eco-physiological phases of insect diapause development justified by transcriptomic profiling. *Proceedings of the National Academy of Sciences of the United States of America*, *114*, 8532–8537. https://doi.org/10.1073/pnas.1707281114

Kreitzman, L., & Foster, R. (2010). *Seasons of Life: The biological rhythms that enable living things to thrive and survive*. Profile Books.

Krofel, M., Špacapan, M., & Jerina, K. (2016). Winter sleep with room service: Denning behaviour of brown bears with access to anthropogenic food. *Journal of Zoology*, *302*(1), 8–14. https://doi.org/10.1111/jzo.12421

Kubrak, O. I., Kučerová, L., Theopold, U., & Nässel, D. R. (2014). The sleeping beauty: How reproductive diapause affects hormone signaling, metabolism, immune response and somatic maintenance in *Drosophila melanogaster*. *PLoS ONE*, *9*, e113051. https://doi.org/10.1371/journal.pone.0113051

Kučerová, L., Kubrak, O. I., Bengtsson, J. M., Strnad, H., Nylin, S., Theopold, U., & Nässel, D. R. (2016). Slowed aging during reproductive dormancy is reflected in genome-wide transcriptome changes in *Drosophila melanogaster*. *BMC Genomics*, *17*, 50. https://doi.org/10.1186/s12864-016-2383-1

Lane, J. E., Czenze, Z. J., Findlay-Robinson, R., & Bayne, E. (2019). Phenotypic plasticity and local adaptation in a wild hibernator evaluated through reciprocal translocation. *The American Naturalist*, *194*, 516–528. https://doi.org/10.1086/702313

Lane, J. E., Kruuk, L. E. B., Charmantier, A., Murie, J. O., Coltman, D. W., Buoro, M., Raveh, S., & Dobson, F. S. (2011). A quantitative genetic analysis of hibernation emergence date in a wild population of Columbian ground squirrels: Quantitative genetics of hibernation emergence. *Journal of Evolutionary Biology*, *24*, 1949–1959. https://doi.org/10.1111/j.1420-9101.2011.02334.x

Lausen, C. L., & Barclay, R. M. R. (2006). Winter bat activity in the Canadian prairies. *Canadian Journal of Zoology*, *84*, 1079–1086. https://doi.org/10.1139/z06-093

Lee, R. E. (2010). A primer on insect cold-tolerance. *Low temperature biology of insects* (pp. 3–34).

Lee, T. M., Pelz, K., Licht, P., & Zucker, I. (1990). Testosterone influences hibernation in golden-mantled ground squirrels. *The American Journal of Physiology*, *259*, R760–R767. https://doi.org/10.1152/ajpregu.1990.259.4.R760

Lehmann, P., Lyytinen, A., Piiroinen, S., & Lindström, L. (2015). Latitudinal differences in diapause related photoperiodic responses of European

Colorado potato beetles (*Leptinotarsa decemlineata*). *Evolutionary Ecology*, *29*, 269–282.

Lehmann, P., Piiroinen, S., Lyytinen, A., & Lindström, L. (2015). Responses in metabolic rate to changes in temperature in diapausing Colorado potato beetle *Leptinotarsa decemlineata* from three European populations. *Physiological Entomology*, *40*, 123–130.

Lehmann, P., Pruisscher, P., Posledovich, D., Carlsson, M., Käkelä, R., Tang, P., Nylin, S., Wheat, C. W., Wiklund, C., & Gotthard, K. (2016). Energy and lipid metabolism during direct and diapause development in a pierid butterfly. *Journal of Experimental Biology*, *219*, 3049–3060.

Levesque, D. L., Nowack, J., & Stawski, C. (2016). Modelling mammalian energetics: The heterothermy problem. *Climate Change Responses*, *3*, 7.

Levin, E., Yom-Tov, Y., Hefetz, A., & Kronfeld-Schor, N. (2013). Changes in diet, body mass and fatty acid composition during pre-hibernation in a subtropical bat in relation to NPY and AgRP expression. *Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology*, *183*, 157–166.

Lisovski, S., Ramenofsky, M., & Wingfield, J. C. (2017). Defining the degree of seasonality and its significance for future research. *Integrative and Comparative Biology*, *57*, 934–942.

Liu, W., Li, Y., Guo, S., Yin, H., Lei, C.-L., & Wang, X.-P. (2016). Association between gut microbiota and diapause preparation in the cabbage beetle: A new perspective for studying insect diapause. *Scientific Reports*, *6*, 38900.

Liu, W., Tan, Q.-Q., Zhu, L., Li, Y., Zhu, F., Lei, C.-L., & Wang, X.-P. (2017). Absence of juvenile hormone signalling regulates the dynamic expression profiles of nutritional metabolism genes during diapause preparation in the cabbage beetle *Colaphellus bowringi*. *Insect Molecular Biology*, *26*, 530–542.

López, C., Eizaguirre, M., & Albajes, R. (1995). Diapause detection and monitoring in the Mediterranean corn stalk borer. *Physiological Entomology*, *20*, 330–336. https://doi.org/10.1111/j.1365-3032.1995.tb00823.x

Lovegrove, B. G. (2017). A phenology of the evolution of endothermy in birds and mammals. *Biological Reviews of the Cambridge Philosophical Society*, *92*, 1213–1240. https://doi.org/10.1111/brv.12280

Lovegrove, B. G., Lobban, K. D., & Levesque, D. L. (2014). Mammal survival at the Cretaceous–Palaeogene boundary: Metabolic homeostasis in prolonged tropical hibernation in tenrecs. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1796), 20141304. https://doi.org/10.1098/rspb.2014.1304

Lozano-Fernandez, J., Carton, R., Tanner, A. R., Puttick, M. N., Blaxter, M., Vinther, J., Olesen, J., Giribet, G., Edgecombe, G. D., & Pisani, D. (2016). A molecular palaeobiological exploration of arthropod terrestrialization. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1699), 20150133. https://doi.org/10.1098/rstb.2015.0133

Lyons, P. J., Lang-Ouellette, D., & Morin, P. J. (2013). CryomiRs: Towards the identification of a cold-associated family of microRNAs. *Comparative Biochemistry and Physiology Part D: Genomics and Proteomics*, *8*, 358–364. https://doi.org/10.1016/j.cbd.2013.10.001

Magnus, T. H., & Henderson, N. E. (1988). Thyroid hormone resistance in hibernating ground squirrels, *Spermophilus richardsoni*: I. Increased binding of triiodo-l-thyronine and l-thyroxine by serum proteins. *General and Comparative Endocrinology*, *69*, 352–360.

Malan, A. (2014). The evolution of mammalian hibernation: Lessons from comparative acid-base physiology. *Integrative and Comparative Biology*, *54*, 484–496. https://doi.org/10.1093/icb/icu002

Martin, S. L., Epperson, L. E., Rose, J. C., Kurtz, C. C., Ane, C., & Carey, H. V. (2008). Proteomic analysis of the winter-protected phenotype of hibernating ground squirrel intestine. *AJP: Regulatory. Integrative and Comparative Physiology*, *295*, R316–R328.

Masaki, S. (2002). Ecophysiological consequences of variability in diapause intensity. *European Journal of Entomology*, *99*, 143–154. https://doi.org/10.14411/eje.2002.022

Mathers, K. E., & Staples, J. F. (2019). Differential posttranslational modification of mitochondrial enzymes corresponds with metabolic suppression during hibernation. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, *317*, R262–R269.

Mayhew, W. W. (1965). Hibernation in the horned lizard, *Phrynosoma m'calli*. *Comparative Biochemistry and Physiology*, *16*, 103–119. https://doi.org/10.1016/0010-406X(65)90167-2

McAllan, B. M., & Geiser, F. (2014). Torpor during reproduction in mammals and birds: Dealing with an energetic conundrum. *Integrative and Comparative Biology*, *54*, 516–532. https://doi.org/10.1093/icb/icu093

McGaugh, S. E., Bronikowski, A. M., Kuo, C.-H., Reding, D. M., Addis, E. A., Flagel, L. E., Janzen, F. J., & Schwartz, T. S. (2015). Rapid molecular evolution across amniotes of the IIS/TOR network. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 7055–7060. https://doi.org/10.1073/pnas.1419659112

McNab, B. K. (2002). *The physiological ecology of vertebrates: A view from energetics*. Cornell University Press.

Melvin, R. G., & Andrews, M. T. (2009). Torpor induction in mammals: Recent discoveries fueling new ideas. *Trends in Endocrinology & Metabolism*, *20*, 490–498. https://doi.org/10.1016/j.tem.2009.09.005

Meyers, P. J., Powell, T. H. Q., Walden, K. K. O., Schieferecke, A. J., Feder, J. L., Hahn, D. A., Robertson, H. M., Berlocher, S. H., & Ragland, G. J. (2016). Divergence of the diapause transcriptome in apple maggot flies: Winter regulation and post-winter transcriptional repression. *The Journal of Experimental Biology*, *219*, 2613–2622. https://doi.org/10.1242/jeb.140566

Moreira, D. C., Venancio, L. P. R., Sabino, M. A. C. T., & Hermes-Lima, M. (2016). How widespread is preparation for oxidative stress in the animal kingdom? *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, Second International Conference on Oxidative Stress in Aquatic Ecosystems*, *200*, 64–78.

Morrow, G., & Nicol, S. C. (2009). Cool sex? Hibernation and reproduction overlap in the Echidna. *PLoS ONE*, *4*, e6070. https://doi.org/10.1371/journal.pone.0006070

Munro, D., & Thomas, D. W. (2004). The role of polyunsaturated fatty acids in the expression of torpor by mammals: A review. *Zoology*, *107*, 29–48. https://doi.org/10.1016/j.zool.2003.12.001

Naya, D. E., Veloso, C., Sabat, P., & Bozinovic, F. (2009). Seasonal flexibility of organ mass and intestinal function for the Andean lizard *Liolaemus nigroviridis*. *Journal of Experimental Zoology. Part A, Ecological Genetics and Physiology*, *311*, 270–277.

Nelson, R. J., Denlinger, D. L., & Somers, D. E. (2010). *Photoperiodism: The biological calendar*. Oxford University Press.

Nelson, R. A., Folk, G. E., Pfeiffer, E. W., Craighead, J. J., Jonkel, C. J., & Steiger, D. L. (1983). Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. *Bears: Their Biology and Management*, *5*, 284–290. https://doi.org/10.2307/3872551

Nicol, S. C., & Morrow, G. E. (2012). Sex and seasonality: Reproduction in the Echidna (*Tachyglossus aculeatus*). In T. Ruf, C. Bieber, W. Arnold, & E. Millesi (Eds.), *Living in a seasonal world: Thermoregulatory and metabolic adaptations* (pp. 143–153). Springer.

Nowack, J., Levesque, D. L., Reher, S., & Dausmann, K. H. (2020). Variable climates lead to varying phenotypes: 'Weird' mammalian torpor and lessons from non-holarctic species. *Frontiers in Ecology and Evolution*, *8*. https://doi.org/10.3389/fevo.2020.00060

Orr, T. J., & Zuk, M. (2013). Does delayed fertilization facilitate sperm competition in bats? *Behavioral Ecology and Sociobiology*, *67*, 1903–1913. https://doi.org/10.1007/s00265-013-1598-2

Oxberry, B. A. (1979). Female reproductive patterns in hibernating bats. *Reproduction*, *56*, 359–367. https://doi.org/10.1530/jrf.0.0560359

Pengelley, E. T., & Asmundson, S. M. (1969). Free-running periods of endogenous circannian rhythms in the golden mantled ground squirrel, *Citellus lateralis*. *Comparative Biochemistry and Physiology*, *30*, 177–183. https://doi.org/10.1016/0010-406X(69)91312-7

Pengelley, E. T., & Fisher, K. C. (1963). The effect of temperature and photoperiod on the yearly hibernating behavior of captive golden-mantled ground squirrels (*Citellus lateralis tescorum*). *Canadian Journal of Zoology*, *41*, 1103–1120. https://doi.org/10.1139/z63-087

Penttinen, O.-P., & Holopainen, I. J. (1992). Seasonal feeding activity and ontogenetic dietary shifts in crucian carp, *Carassius carassius*. *Environmental Biology of Fishes*, *33*, 215–221. https://doi.org/10.1007/BF00002566

Pigeon, K. E., Stenhouse, G., & Côté, S. D. (2016). Drivers of hibernation: Linking food and weather to denning behaviour of grizzly bears. *Behavioral Ecology and Sociobiology*, *70*, 1745–1754. https://doi.org/10.1007/s00265-016-2180-5

Posledovich, D., Toftegaard, T., Wiklund, C., Ehrlén, J., & Gotthard, K. (2015). Latitudinal variation in diapause duration and post-winter development in two pierid butterflies in relation to phenological specialization. *Oecologia*, *177*, 181–190. https://doi.org/10.1007/s00442-014-3125-1

Powell, T. H. Q., Nguyen, A., Xia, Q., Feder, J. L., Ragland, G. J., & Hahn, D. A. (2020). A rapidly evolved shift in life history timing during ecological speciation is driven by the transition between developmental phases. *Journal of Evolutionary Biology*, *33*(10), 1371–1386. https://doi.org/10.1111/jeb.13676

Pruisscher, P., Nylin, S., Gotthard, K., & Wheat, C. W. (2018). Genetic variation underlying local adaptation of diapause induction along a cline in a butterfly. *Molecular Ecology*, *27*(18), 3613–3626. https://doi.org/10.1111/mec.14829

Racey, P. A. (1973). Environmental factors affecting the length of gestation in heterothermic bats. *Journal of Reproduction and Fertility*. Supplement, *19*, 175–189.

Ragland, G. J., Egan, S. P., Feder, J. L., Berlocher, S. H., & Hahn, D. A. (2011). Developmental trajectories of gene expression reveal candidates for diapause termination: A key life-history transition in the apple maggot fly *Rhagoletis pomonella*. *Journal of Experimental Biology*, *214*, 3948–3960. https://doi.org/10.1242/jeb.061085

Ragland, G. J., & Keep, E. (2017). Comparative transcriptomics support evolutionary convergence of diapause responses across Insecta. *Physiological Entomology*, *42*, 246–256. https://doi.org/10.1111/phen.12193

Richter, M. M., Barnes, B. M., O'Reilly, K. M., Fenn, A. M., & Buck, C. L. (2016). The influence of androgens on hibernation phenology of free-living male arctic ground squirrels. *Hormones and Behavior*, *89*, 92–97. https://doi.org/10.1016/j.yhbeh.2016.12.007

Rismiller, P. D., & McKelvey, M. W. (2000). Spontaneous arousal in reptiles? Body temperature ecology of Rosenberg's Goanna, *Varanus rosenbergi*. In G. Heldmaier & M. Klingenspor (Eds.), *Life in the cold* (pp. 57–64). Springer.

Ruf, T., & Arnold, W. (2008). Effects of polyunsaturated fatty acids on hibernation and torpor: A review and hypothesis. *American Journal of Physiology – Regulatory, Integrative and Comparative Physiology*, *294*, R1044–R1052.

Ruf, T., & Geiser, F. (2015). Daily torpor and hibernation in birds and mammals. *Biological Reviews*, *90*, 891–926. https://doi.org/10.1111/brv.12137

Ryan, S. F., Valella, P., Thivierge, G., Aardema, M. L., & Scriber, J. M. (2018). The role of latitudinal, genetic and temperature variation in the induction of diapause of *Papilio glaucus* (Lepidoptera: Papilionidae). *Insect Science*, *25*, 328–336.

Schiesari, L., & O'Connor, M. B. (2013). Chapter eight – Diapause: Delaying the developmental clock in response to a changing environment. In A. E. Rougvie & M. B. O'Connor (Eds.). *Current topics in developmental biology, developmental timing* (Vol. 105, pp. 213–246). Academic Press.

Schmidt, P. S., Paaby, A. B., & Heschel, M. S. (2005). Genetic variance for diapause expression and associated life histories in drosophila melanogaster. *Evolution*, *59*, 2616–2625. https://doi.org/10.1111/j.0014-3820.2005.tb00974.x

Schwartz, C., Hampton, M., & Andrews, M. T. (2013). Seasonal and regional differences in gene expression in the brain of a hibernating mammal. *PLoS ONE*, *8*, e58427.

Schwartz, C., Hampton, M., & Andrews, M. T. (2015). Hypothalamic gene expression underlying pre-hibernation satiety: Gene expression in natural satiety. *Genes, Brain and Behavior*, *14*, 310–318. https://doi.org/10.1111/gbb.12199

Secor, S. M., & Carey, H. V. (2016). Integrative physiology of fasting. In R. Terjung (Ed.), *Comprehensive physiology* (pp. 773–825). John Wiley & Sons Inc.

Seebacher, F. (2005). A review of thermoregulation and physiological performance in reptiles: What is the role of phenotypic flexibility? *Journal of Comparative Physiology B*, *175*, 453–461. https://doi.org/10.1007/s00360-005-0010-6

Seebacher, F. (2018). The evolution of metabolic regulation in animals. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, *224*, 195–203. https://doi.org/10.1016/j.cbpb.2017.11.002

Seymour, R. S. (1973). Energy metabolism of dormant spadefoot toads (Scaphiopus). *Copeia*, *1973*, 435–445. https://doi.org/10.2307/1443107

Sim, C., & Denlinger, D. L. (2008). Insulin signaling and FOXO regulate the overwintering diapause of the mosquito Culex pipiens. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 6777–6781. https://doi.org/10.1073/pnas.0802067105

Sim, C., & Denlinger, D. L. (2013). Insulin signaling and the regulation of insect diapause. *Frontiers in Physiology*, *4*. https://doi.org/10.3389/fphys.2013.00189

Simons, M. J. P. (2009). The evolution of the cyanobacterial posttranslational clock from a primitive 'phoscillator'. *Journal of Biological Rhythms*, *24*, 175–182. https://doi.org/10.1177/0748730409333953

Sinclair, B. J., Vernon, P., Jaco Klok, C., & Chown, S. L. (2003). Insects at low temperatures: An ecological perspective. *Trends in Ecology & Evolution*, *18*, 257–262. https://doi.org/10.1016/S0169-5347(03)00014-4

Sláma, K., & Denlinger, D. L. (1992). Infradian cycles of oxygen consumption in diapausing pupae of the flesh fly, *Sarcophaga crassipalpis*, monitored by a scanning microrespirographic method. *Archives of Insect Biochemistry and Physiology*, *20*, 135–143.

Sommer, F., Ståhlman, M., Ilkayeva, O., Arnemo, J. M., Kindberg, J., Josefsson, J., Newgard, C. B., Fröbert, O., & Bäckhed, F. (2016). The gut microbiota modulates energy metabolism in the hibernating brown bear *Ursus arctos*. *Cell Reports*, *14*, 1655–1661. https://doi.org/10.1016/j.celrep.2016.01.026

Sparkman, A. M., Schwartz, T. S., Madden, J. A., Boyken, S. E., Ford, N. B., Serb, J. M., & Bronikowski, A. M. (2012). Rates of molecular evolution vary in vertebrates for insulin-like growth factor-1 (IGF-1), a pleiotropic locus that regulates life history traits. *General and Comparative Endocrinology*, *178*, 164–173. https://doi.org/10.1016/j.ygcen.2012.04.022

Staples, J. F. (2016). Metabolic flexibility: Hibernation, torpor, and estivation. In R. Terjung (Ed.), *Comprehensive physiology* (pp. 737–771). John Wiley & Sons Inc.

Stark, G., Tamar, K., Itescu, Y., Feldman, A., & Meiri, S. (2018). Cold and isolated ectotherms: Drivers of reptilian longevity. *Biological Journal of the Linnean Society*, *125*, 730–740. https://doi.org/10.1093/biolinnean/bly153

Storey, J. M., & Storey, K. B. (2004). Cold hardiness and freeze tolerance. In K. B. Storey (Ed.), *Functional metabolism* (pp. 473–503). John Wiley & Sons Inc.

Storey, K. B. (2002). Life in the slow lane: Molecular mechanisms of estivation. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *133*, 733–754. https://doi.org/10.1016/S1095-6433(02)00206-4

Storey, K. B. (2003). Mammalian hibernation. Transcriptional and translational controls. *Advances in Experimental Medicine and Biology*, *543*, 21–38.

Storey, K. B. (2010). Out cold: Biochemical regulation of mammalian hibernation – A mini-review. *Gerontology*, *56*, 220–230. https://doi.org/10.1159/000228829

Storey, K. B., & Storey, J. M. (2012). Aestivation: Signaling and hypometabolism. *The Journal of Experimental Biology*, *215*, 1425–1433. https://doi.org/10.1242/jeb.054403

Storey, K. B., & Storey, J. M. (2013). Molecular biology of freezing tolerance. *Comprehensive Physiology*, *3*(3), 1283–1308). https://doi.org/10.1002/cphy.c130007

Sunday, J. M., Bates, A. E., & Dulvy, N. K. (2011). Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society B: Biological Sciences*, *278*, 1823–1830. https://doi.org/10.1098/rspb.2010.1295

Tannenbaum, M. G., & Pivorun, E. B. (1984). Differences in daily torpor patterns among three southeastern species ofPeromyscus. *Journal of Comparative Physiology B*, *154*, 233–236. https://doi.org/10.1007/BF02464401

Tannenbaum, M. G., & Pivorun, E. B. (1988). Seasonal study of daily torpor in southeastern *Peromyscus maniculatus* and *Peromyscus leucopus* from mountains and foothills. *Physiological Zoology*, *61*, 10–16. https://doi.org/10.1086/physzool.61.1.30163731

Tatar, M., Chien, S. A., & Priest, N. K. (2001). Negligible senescence during reproductive dormancy in *Drosophila melanogaster*. *The American Naturalist*, *158*, 248–258.

Tatar, M., & Yin, C.-M. (2001). Slow aging during insect reproductive diapause: Why butterflies, grasshoppers and flies are like worms. *Experimental Gerontology, Slowly Aging Organisms*, *36*, 723–738. https://doi.org/10.1016/S0531-5565(00)00238-2

Tauber, C. A., & Tauber, M. J. (1981). Insect seasonal cycles: Genetics and evolution. *Annual Review of Ecology and Systematics*, *12*, 281–308. https://doi.org/10.1146/annurev.es.12.110181.001433

Tauber, M. J., & Tauber, C. A. (1976). Insect seasonality: Diapause maintenance, termination, and postdiapause development. *Annual Review of Entomology*, *21*, 81–107. https://doi.org/10.1146/annurev.en.21.010176.000501

Tauber, M., Tauber, C., & Masaki, S. (1985). *Seasonal adaptations of insects*. Oxford University Press.

Tessier, S. N., Zhang, J., Biggar, K. K., Wu, C.-W., Pifferi, F., Perret, M., & Storey, K. B. (2015). Regulation of the PI3K/AKT pathway and fuel utilization during primate torpor in the gray mouse lemur, *Microcebus murinus*. *Genomics, Proteomics & Bioinformatics*, *13*, 91–102. https://doi.org/10.1016/j.gpb.2015.03.006

Thomas, D. W., Brock Fenton, M., & Barclay, R. M. R. (1979). Social behavior of the little brown bat, *Myotis lucifugus*. *Behavioral Ecology and Sociobiology*, *6*, 129–136. https://doi.org/10.1007/BF00292559

Tøien, Ø., Blake, J., Edgar, D. M., Grahn, D. A., Heller, H. C., & Barnes, B. M. (2011). Hibernation in black bears: Independence of metabolic suppression from body temperature. *Science*, *331*, 906–909. https://doi.org/10.1126/science.1199435

Toxopeus, J., & Sinclair, B. J. (2018). Mechanisms underlying insect freeze tolerance. *Biological Reviews*, *93*, 1891–1914. https://doi.org/10.1111/brv.12425

Treat, M. D., Scholer, L., Barrett, B., Khachatryan, A., McKenna, A. J., Reyes, T., Rezazadeh, A., Ronkon, C. F., Samora, D., Santamaria, J. F., Silva Rubio, C., Sutherland, E., Richardson, J., Lighton, J. R. B., & van Breukelen, F. (2018). Extreme physiological plasticity in a hibernating basoendothermic mammal, *Tenrec ecaudatus*. *The Journal of Experimental Biology*, *221*, jeb185900.

Turbill, C. (2008). Winter activity of Australian tree-roosting bats: Influence of temperature and climatic patterns. *Journal of Zoology*, *276*, 285–290. https://doi.org/10.1111/j.1469-7998.2008.00487.x

Turbill, C., Bieber, C., & Ruf, T. (2011). Hibernation is associated with increased survival and the evolution of slow life histories among mammals. *Proceedings of the Royal Society B: Biological Sciences*, *278*, 3355–3363. https://doi.org/10.1098/rspb.2011.0190

Turbill, C., & Geiser, F. (2008). Hibernation by tree-roosting bats. *Journal of Comparative Physiology B, Biochemical, Systemic, and Environmental Physiology*, *178*, 597–605. https://doi.org/10.1007/s00360-007-0249-1

Turbill, C., & Prior, S. (2016). Thermal climate-linked variation in annual survival rate of hibernating rodents: Shorter winter dormancy and lower survival in warmer climates. *Functional Ecology*, *30*, 1366–1372. https://doi.org/10.1111/1365-2435.12620

Turbill, C., Ruf, T., Smith, S., & Bieber, C. (2013). Seasonal variation in telomere length of a hibernating rodent. *Biology Letters*, *9*, 20121095. https://doi.org/10.1098/rsbl.2012.1095

Ultsch, G. R. (1989). Ecology and physiology of hibernation and overwintering among freshwater fishes, turtles, and snakes. *Biological Reviews*, *64*, 435–515. https://doi.org/10.1111/j.1469-185X.1989.tb00683.x

van Breukelen, F., & Martin, S. L. (2002). Invited Review: Molecular adaptations in mammalian hibernators: Unique adaptations or generalized responses? *Journal of Applied Physiology*, *92*, 2640–2647. https://doi.org/10.1152/japplphysiol.01007.2001

van Breukelen, F., & Martin, S. L. (2015). The hibernation continuum: Physiological and molecular aspects of metabolic plasticity in mammals. *Physiology*, *30*, 273–281. https://doi.org/10.1152/physiol.00010.2015

Vermunt, A. M. W., Koopmanschap, A. B., Vlak, J. M., & de Kort, C. A. D. (1999). Expression of the juvenile hormone esterase gene in the Colorado potato beetle, *Leptinotarsa decemlineata*: Photoperiodic and juvenile hormone analog response. *Journal of Insect Physiology*, *45*, 135–142. https://doi.org/10.1016/S0022-1910(98)00107-3

Vornanen, M. (2011). Seasonal adaptation of crucian carp (*Carassius carassius* L.) heart: Glycogen stores and lactate dehydrogenase activity. *Canadian Journal of Zoology*, *72*(3), 433–442.

Vornanen, M., & Paajanen, V. (2006). Seasonal changes in glycogen content and Na+-K+-ATPase activity in the brain of crucian carp. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, *291*, R1482–R1489.

Vornanen, M., Stecyk, J. A. W., & Nilsson, G. E. (2009). Chapter 9: The anoxia-tolerant crucian carp (*Carassius carassius* L.). In J. G. Richards, A. P. Farrell, & C. J. Brauner (Eds.), *Fish physiology* (Vol. 27, pp. 397–441). Elsevier.

Wadsworth, C. B., Woods, W. A., Hahn, D. A., & Dopman, E. B. (2013). One phase of the dormancy developmental pathway is critical for the evolution of insect seasonality. *Journal of Evolutionary Biology*, *26*, 2359–2368. https://doi.org/10.1111/jeb.12227

Wang, T., Geng, S.-L., Guan, Y.-M., & Xu, W.-H. (2018). Deacetylation of metabolic enzymes by Sirt2 modulates pyruvate homeostasis to extend insect lifespan. *Aging*, *10*, 1053–1072. https://doi.org/10.18632/aging.101447

Wheeler, D. E., & Nijhout, H. F. (2003). A perspective for understanding the modes of juvenile hormone action as a lipid signaling system. *BioEssays*, *25*, 994–1001. https://doi.org/10.1002/bies.10337

Whitaker, J. O., & Rissler, L. J. (1992). Winter activity of bats at a mine entrance in Vermillion County, Indiana. *The American Midland Naturalist*, *127*, 52–59. https://doi.org/10.2307/2426321

Whitaker, J. O., & Rissler, L. J. (1993). Do bats feed in winter? *The American Midland Naturalist*, *129*, 200–203. https://doi.org/10.2307/2426448

Whiteman, J. P., Harlow, H. J., Durner, G. M., Anderson-Sprecher, R., Albeke, S. E., Regehr, E. V., Amstrup, S. C., & Ben-David, M. (2015). Summer declines in activity and body temperature offer polar bears limited energy savings. *Science*, *349*, 295–298. https://doi.org/10.1126/science.aaa8623

Wiens, J. J., Lapoint, R. T., & Whiteman, N. K. (2015). Herbivory increases diversification across insect clades. *Nature Communications*, *6*, 8370. https://doi.org/10.1038/ncomms9370

Wijenayake, S., Luu, B. E., Zhang, J., Tessier, S. N., Quintero-Galvis, J. F., Gaitán-Espitia, J. D., Nespolo, R. F., & Storey, K. B. (2018). Strategies of biochemical adaptation for hibernation in a South American marsupial *Dromiciops gliroides*: 1. Mitogen-activated protein kinases and the cell stress response. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, *224*, 12–18.

Wilkinson, A., Hloch, A., Mueller-Paul, J., & Huber, L. (2017). The effect of brumation on memory retention. *Scientific Reports*, *7*, 40079. https://doi.org/10.1038/srep40079

Williams, C. T., Barnes, B. M., Kenagy, G. J., & Buck, C. L. (2014). Phenology of hibernation and reproduction in ground squirrels: Integration of environmental cues with endogenous programming: Annual rhythms of squirrels. *Journal of Zoology*, *292*, 112–124. https://doi.org/10.1111/jzo.12103

Williams, C. T., Buck, C. L., Sheriff, M. J., Richter, M. M., Krause, J. S., & Barnes, B. M. (2017). Sex-dependent phenological plasticity in an arctic hibernator. *The American Naturalist*, *190*, 854–859. https://doi.org/10.1086/694320

Williams, C. M., Ragland, G. J., Betini, G., Buckley, L. B., Cheviron, Z. A., Donohue, K., Hereford, J., Humphries, M. M., Lisovski, S., Marshall, K. E., Schmidt, P. S., Sheldon, K. S., Varpe, Ø., & Visser, M. E. (2017). Understanding evolutionary impacts of seasonality: An introduction to the symposium. *Integrative and Comparative Biology*, *57*, 921–933. https://doi.org/10.1093/icb/icx122

Williams, K. D., Busto, M., Suster, M. L., So, A.-K.-C., Ben-Shahar, Y., Leevers, S. J., & Sokolowski, M. B. (2006). Natural variation in Drosophila melanogaster diapause due to the insulin-regulated PI3-kinase. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 15911–15915. https://doi.org/10.1073/pnas.0604592103

Willis, C. K. R. (2017). Trade-offs influencing the physiological ecology of hibernation in temperate-zone bats. *Integrative and Comparative Biology*, *57*, 1214–1224. https://doi.org/10.1093/icb/icx087

Willis, C. K. R., Brigham, R. M., & Geiser, F. (2006). Deep, prolonged torpor by pregnant, free-ranging bats. *Naturwissenschaften*, *93*, 80–83. https://doi.org/10.1007/s00114-005-0063-0

Wimsatt, W. A. (1969). Some interrelations of reproduction and hibernation in mammals. *Symposia of the Society for Experimental Biology*, *23*, 511–549.

Withers, P. C., & Cooper, C. E. (2010). Metabolic depression: A historical perspective. In C. Arturo Navas & J. E. Carvalho (Eds.), *Aestivation: Molecular and physiological aspects, progress in molecular and subcellular biology* (pp. 1–23). Springer.

Wolkow, C. A., Kimura, K. D., Lee, M.-S., & Ruvkun, G. (2000). Regulation of *C. elegans* life-span by insulin like signaling in the nervous system. *Science*, *290*, 147–150.

Wooding, J. B., & Hardisky, T. S. (1992). Denning by black bears in Northcentral Florida. *Journal of Mammalogy*, *73*, 895–898. https://doi.org/10.2307/1382213

Woods, C. P., & Brigham, R. M. (2004). The avian enigma: 'Hibernation' by common poorwills (*Phalaenoptilus nuttallii*). In B. M. Barnes & H. V. Carey (Eds.), *Life in the cold: evolution, mechanisms, adaptation, and application* (pp. 129–138). Twelfth International Hibernation Symposium. Institute of Arctic Biology, University of Alaska Fairbanks, USA.

Woods, C. P., Czenze, Z. J., & Brigham, R. M. (2019). The avian 'hibernation' enigma: Thermoregulatory patterns and roost choice of the common poorwill. *Oecologia*, *189*, 47–53. https://doi.org/10.1007/s00442-018-4306-0

Wright, P. A., Obbard, M. E., Battersby, B. J., Felskie, A. K., LeBlanc, P. J., & Ballantyne, J. S. (1999). Lactation during hibernation in wild black bears: Effects on plasma amino acids and nitrogen metabolites. *Physiological and Biochemical Zoology*, *72*, 597–604. https://doi.org/10.1086/316691

Xu, W.-H., Lu, Y.-X., & Denlinger, D. L. (2012). Cross-talk between the fat body and brain regulates insect developmental arrest. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 14687–14692. https://doi.org/10.1073/pnas.1212879109

Yamada, N., & Mizoguchi, A. (2017). Endocrine changes during diapause development in the cabbage army moth Mamestra brassicae. *Physiological Entomology*, *42*, 239–245.

Zervanos, S. M., Maher, C. R., Waldvogel, J. A., & Florant, G. L. (2010). Latitudinal differences in the hibernation characteristics of woodchucks (*Marmota monax*). *Physiological and Biochemical Zoology*, *83*, 135–141.

Zhang, Q., & Denlinger, D. L. (2012). Dynamics of diapause hormone and prothoracicotropic hormone transcript expression at diapause termination in pupae of the corn earworm, *Helicoverpa zea*. *Peptides*, *Invertebrate Neuropeptides XII*, *34*, 120–126. https://doi.org/10.1016/j.peptides.2011.05.019

DATA SOURCES

Agugliaro, J. (2011). *Ecophysiology of hibernation in timer rattlesnakes (*Crotalus horridus*)*. University of Arkansas.

Beecham, J. J., Reynolds, D. G., & Hornocker, M. G. (1983). Black bear denning activities and den characteristics in west-central Idaho. *Bears: Their Biology and Management*, *5*, 79–86. https://doi.org/10.2307/3872522

Bradshaw, W. E., & Lounibos, L. P. (1977). Evolution of dormancy and its photoperiodic control in pitcher-plant mosquitoes. *Evolution*, *31*, 546. https://doi.org/10.2307/2407521

Bradshaw, W. E., Quebodeaux, M. C., & Holzapfel, C. M. (2003). Circadian rhythmicity and photoperiodism in the pitcher-plant mosquito: Adaptive response to the photic environment or correlated response to the seasonal environment? *The American Naturalist*, *161*, 735–748. https://doi.org/10.1086/374344

Chaplin, S. B., & Wells, P. H. (1982). Energy reserves and metabolic expenditures of monarch butterflies overwintering in southern California. *Ecological Entomology*, *7*, 249–256. https://doi.org/10.1111/j.1365-2311.1982.tb00664.x

Clegg, J. (1997). Embryos of *Artemia franciscana* survive four years of continuous anoxia: The case for complete metabolic rate depression. *Journal of Experimental Biology*, *200*, 467–475.

Clegg, J. S., Drinkwater, L. E., & Sorgeloos, P. (1996). The metabolic status of diapause embryos of *Artemia franciscana* (SFB). *Physiological Zoology*, *69*, 49–66.

Elvert, R., & Heldmaier, G. (2005). Cardiorespiratory and metabolic reactions during entrance into torpor in dormice, *Glis glis*. *Journal of Experimental Biology*, *208*, 1373–1383. https://doi.org/10.1242/jeb.01546

Ernst, C. H., Orr, J. M., Creque, T. R., Laemmerzahl, A. F., & Hartsell, T. D. (2012). Annual and daily activity cycles of snakes in northern Virginia, USA – British Herpetological Society. *Herpetological Bulletin*, 23–28.

Evans, K. W., & Brust, R. A. (1972). Induction and termination of diapause in *Wyeomyia smithii* (diptera: culicidae), and larval survival studies at low and subzero temperatures1. *The Canadian Entomologist*, *104*, 1937–1950.

Ferron, J. (1996). How do woodchucks (*Marmota monax*) cope with harsh winter conditions? *Journal of Mammalogy*, *77*, 412–416. https://doi.org/10.2307/1382817

Fitch, H. S. (1963). Natural history of the black rat snake (*Elaphe o. obsoleta*) in Kansas. *Copeia*, *1963*, 649–658. https://doi.org/10.2307/1440967

Game Division, Maine Department of Inland Fisheries and Game, and Maine Department of Inland Fisheries and Wildlife. (1961). *The Black Bear and its Status in Maine*, *1961*. Resource Management Documents.

Goebel, C., Stevens, S., Dennison, C., & Harveson, P. M. (2016). Black bear denning behavior in the chisos mountains of big bend national park. *Texas Wildlife: Borderlands News*, 38–40.

Goodrich, J. M., & Berger, J. (1994). Winter recreation and hibernating black bears *Ursus americanus*. *Biological Conservation*, *67*, 105–110. https://doi.org/10.1016/0006-3207(94)90354-9

Graber, D. M. (1990). Winter behavior of black bears in the Sierra Nevada, California. *Bears: Their Biology and Management*, *8*, 269–272. https://doi.org/10.2307/3872928

Gregory, P. T. (1982). Reptilian hibernation. *Biology of the Reptilia*, *13*, 53–154.

Hamilton, R. J., & Marchinton, R. L. (1980). Denning and related activities of black bears in the coastal plain of North Carolina. *Bears: Their Biology and Management*, *4*, 121–126. https://doi.org/10.2307/3872854

Hellgren, E. C., & Vaughan, M. R. (1987). Home range and movements of winter-active black bears in the great dismal swamp. *Bears: Their Biology and Management*, *7*, 227–234. https://doi.org/10.2307/3872629

Immell, D., Jackson, D. H., & Boulay, M. C. (2013). Denning ecology of American black bears in the Cascade Mountains of western Oregon. *Ursus*, *24*, 1–12. https://doi.org/10.2192/URSUS-D-11-00008.1

John-Alder, H. B. (1984). Seasonal variations in activity, aerobic energetic capacities, and plasma thyroid hormones (T3 and T4) in an iguanid lizard. *Journal of Comparative Physiology B*, *154*, 409–419. https://doi.org/10.1007/BF00684448

Johnson, K. G., & Pelton, M. R. (1980). Environmental relationships and the denning period of black bears in Tennessee. *Journal of Mammalogy*, *61*, 653–660. https://doi.org/10.2307/1380310

Jonkel, C. J., & Cowan, I. M. (1971). The black bear in the spruce-fir forest. *Wildlife Monographs*, *27*, 3–57.

Kasbohm, J. W. (1994). *Response of black bears to gypsy moth infestation in Shenandoah National Park, Virginia*. Virginia Tech.

Kolenosky, G. B., & Strathearn, S. M. (1987). Winter denning of black bears in East-Central Ontario. *Bears: Their Biology and Management*, *7*, 305–316. https://doi.org/10.2307/3872637

LeCount, A. L. (1980). Some aspects of black bear ecology in the Arizona Chaparral. *Bears: Their Biology and Management*, *4*, 175–179. https://doi.org/10.2307/3872864

Lindzey, F. G., & Meslow, E. C. (1976). Winter dormancy in black bears in Southwestern Washington. *The Journal of Wildlife Management*, *40*, 408–415.

Manville, A. M. (1987). Den selection and use by black bears in Michigan's northern lower Peninsula. *Bears: Their Biology and Management*, *7*, 317–322. https://doi.org/10.2307/3872638

Mullin, S., Gutzke, W., Zenitsky, G., & Cooper, R. (2000). *Home ranges of rat snakes (Colubridae: Elaphe) in different habitats*. Faculty Publications.

Nordberg, E. J. (2013). *Thermal ecology and behavioral activity in hibernating timber rattlesnakes* (Crotalus horridus) (PhD Thesis). Middle Tennessee State University.

O'Pezio, J., Clarke, S. H., & Hackford, C. (1983). Chronology of black bear denning in the catskill region of New York. *Bears: Their Biology and Management*, *5*, 87–93. https://doi.org/10.2307/3872523

Rogers, L. L. (1987). Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. *Wildlife Monographs*, *97*, 3–72.

Schwartz, C. C., Miller, S. D., & Franzmann, A. W. (1987). Denning ecology of three black bear populations in Alaska. *Bears: Their Biology and Management*, *7*, 281–291. https://doi.org/10.2307/3872635

Sexton, O. J., & Hunt, S. R. (1980). Temperature relationships and movements of snakes (*Elaphe obsoleta*, Coluber constrictor) in a cave Hibernaculum. *Herpetologica*, *36*, 20–26.

Smith, M. E., Hechtel, J. L., & Follmann, E. H. (1994). Black bear denning ecology in interior Alaska. *Bears: Their Biology and Management*, *9*, 513–522. https://doi.org/10.2307/3872739

Smith, S. M., & Brust, R. A. (1971). Photoperiodic control of the maintenance and termination of larval diapause in *Wyeomyia smithii* (Coq.) (Diptera: Culicidae) with notes on oogenesis in the adult female. *Canadian Journal of Zoology*, *49*, 1065–1073.

Smith, T. R. (1986). Activity and behavior of denned black bears in the lower Mississippi River Valley. *Bears: Their Biology and Management*, *6*, 137–143. https://doi.org/10.2307/3872817

Sperry, J. H., Blouin-Demers, G., Carfagno, G. L. F., & Weatherhead, P. J. (2010). Latitudinal variation in seasonal activity and mortality in ratsnakes (*Elaphe obsoleta*). *Ecology*, *91*, 1860–1866. https://doi.org/10.1890/09-1154.1

Stickel, L. F., Stickel, W. H., & Schmid, F. C. (1980). Ecology of a Maryland population of black rat snakes (*Elaphe o. obsoleta*). *The American Midland Naturalist*, *103*, 1–14. https://doi.org/10.2307/2425033

Tietje, W. D., & Ruff, R. L. (1980). Denning behavior of black bears in boreal forest of Alberta. *The Journal of Wildlife Management*, *44*, 858–870. https://doi.org/10.2307/3808314

Tsuji, J. S. (1988). Seasonal profiles of standard metabolic rate of lizards (*Sceloporus occidentalis*) in relation to latitude. *Physiological Zoology*, *61*, 230–240. https://doi.org/10.1086/physzool.61.3.30161236

Waller, B. W., Belant, J. L., Young, B. W., Leopold, B. D., & Simek, S. L. (2012). Denning chronology and den characteristics of American black bears in Mississippi. *Ursus*, *23*, 6–11. https://doi.org/10.2192/URSUS-D-11-00014.1

Weatherhead, P. J. (1989). Temporal and thermal aspects of hibernation of black rat snakes (*Elaphe obsoleta*) in Ontario. *Canadian Journal of Zoology*, *67*, 2332–2335.

Weaver, K. M., & Pelton, M. R. (1994). Denning ecology of black bears in the tensas river basin of Louisiana. *Bears: Their Biology and Management*, *9*, 427–433. https://doi.org/10.2307/3872729

Wilz, M., & Heldmaier, G. (2000). Comparison of hibernation, estivation and daily torpor in the edible dormouse, *Glis glis*. *Journal of Comparative Physiology B*, *170*, 511–521. https://doi.org/10.1007/s003600000129

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Wilsterman K, Ballinger MA, Williams CM. A unifying, eco-physiological framework for animal dormancy. *Funct Ecol*. 2021;35:11–31. https://doi.org/10.1111/1365-2435.13718