

ECOGRAPHY

Review

Life history consequences of climate change in hibernating mammals: a review

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Climatic shifts to warmer and often drier conditions are challenging terrestrial species worldwide. These shifts are occurring more rapidly at higher elevations and latitudes, likely causing disproportionate effects to mammalian hibernators there. While there is some information about how these species' ranges are responding to climatic shifts, we lack an understanding of how climate components are affecting species' life history variation, which is key to individual success and population-level resilience. We reviewed the literature to identify the direction of life history responses to climate change in mammalian hibernators along three axes: latitudinal, elevational and temporal. We found 39 studies involving 27 species that reported climate effects on our four target life history traits – phenology, body mass/condition and growth, reproduction and survival. We found warmer temperatures are advancing hibernator phenology and increasing reproductive success. By contrast, warming and drying trends are having uncertain effects on body condition, and complex effects on survival – depending on season, age class, latitude and elevation. We found no pattern of significant climate-trait outcomes by duration or decade of study. More research on drought conditions – particularly in relation to resource availability – would help inform hibernator susceptibility to increased drying trends expected to intensify globally. Notably, our results are highly biased towards small mammal hibernators in Northern Hemisphere alpine/mountain ecosystems, with few long-term studies conducted on Southern Hemisphere hibernators. This review highlights that phenological shifts constitute one of the most obvious consequences of climate change, yet, the timing of life history events (e.g. timing of migration, reproduction, hibernation) remains poorly understood. Further integration of insights from physiologists, evolutionary biologists and population ecologists working on wild populations will improve our collective understanding of the effects of seasonal climatic shifts on mammalian hibernator life history traits, key drivers of their population-level persistence.

Keywords: body mass, climate change, conservation, elevation, evolution, global warming, growth, hibernation, life history, phenology, reproduction, survival



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Introduction

Over recent decades we have amassed information on how climate change impacts biodiversity (Rinawati et al. 2013, Newbold 2018, Nunez et al. 2019), by shifting species distributions (Parmesan and Yohe 2003, Chen et al. 2011, Lenoir and Svenning 2015), driving population declines (Both et al. 2010, Spooner et al. 2018, Halsch et al. 2021) and increasing susceptibility to local extinction (Thomas et al. 2004, Urban 2015, Román-Palacios and Wiens 2020). Typically, effects of climate change on individual species are projected using species distribution models, which incorporate climatic variables and species presence/absence data (Porfiriio et al. 2014). However, these models rarely consider variability in the life history traits that underlie individual success and population-level resilience (Urban et al. 2016), and they show limited success in accurately predicting population biology (Lee-Yaw et al. 2021). Fortunately, long-term studies that examine the mechanisms that govern wildlife responses to climate change have been on the rise (Boutin and Lane 2014, Selwood et al. 2015). These studies reveal how animals respond to a changing climate, via shifts in behavioral traits (Bastille-Rousseau et al. 2018), physiological states (Naya et al. 2017) and vital rates (Cordes et al. 2020).

Among animals, species susceptibility can vary depending on location, thermal niche or other traits. Often living at high elevation and high latitudes, hibernating species are thought to be particularly susceptible to climate change (Geiser 2013). Mountain surface air temperature observations in western North America, European Alps and High Mountain Asia show warming over recent decades at an average rate of $0.3 \pm 0.2^\circ\text{C}$ per decade, thereby outpacing the global warming rate of $0.2^\circ \pm 0.1^\circ\text{C}$ per decade (IPCC 2018). Warming temperatures in temperate and polar regions are shifting vegetative growing seasons and phenological events (Iler et al. 2013, CaraDonna et al. 2014, Prev  y et al. 2017), thereby impacting resources available to hibernators (Ruf and Geiser 2015).

Hibernation is an energetic tactic of heterothermy used to reduce metabolic costs during periods of low ambient temperatures or food scarcity (Humphries et al. 2003, Geiser 2013). It is characterized by multi-day bouts of torpor (periods of reduced metabolic rate), generally interspersed with brief arousals to normal body temperatures (Jastroch et al. 2016). Hibernation is physiologically distinct from short bouts of torpor (Geiser and Ruf 1995), though the two tactics may also be represented as different points in a continuum in non-Holarctic heterothermic species (Nowack et al. 2020). Fitness consequences of climate change on true hibernators may similarly be distinct from daily heterotherms (i.e. species employing torpor; Geiser and Ruf 1995) for three main reasons. First, short bouts of torpor are controlled by endogenous circadian rhythms, but hibernation is not (Ruf and Geiser 2015), suggesting that hibernators could be more sensitive than daily heterotherms to the environmental context experienced, such as reducing total hibernation time or torpor bout duration in response to higher or lower

ambient temperatures (Geiser and Kenagy 1988, Geiser 2021). Second, hibernators are also on average heavier than daily heterotherms, reflecting a different energy storage tactic that may impact other performance variables (Ruf and Geiser 2015). For example, hibernators have long gestation periods that impinge on a short active season, where breeding has to be timed with high quality resource availability to satisfy lactation demands, making them extremely susceptible to phenological mismatches (Boutin and Lane 2014). Third, hibernators also occupy higher average latitudes than do daily heterotherms (35°N versus 25°N , Ruf and Geiser 2015), and tend to live at the higher elevations that climate change is disproportionately impacting. However, these two categories of heterothermy are not mutually exclusive, as true hibernators may also use bouts of torpor as an energy-saving strategy (e.g. edible dormouse *Glis glis*, Fietz et al. 2004).

Studies focused on mammalian hibernators have shown significant shifts in life history traits (e.g. phenology of hibernation) and vital rates (e.g. over-winter survival rates) in response to climate change (Lane et al. 2012, R  zouki et al. 2016, Cordes et al. 2020). These life history and demographic responses may occur for a number of reasons specific to mammalian hibernators, including limited dispersal ability (Schloss et al. 2012), reduced metabolic ability to hibernate with warming-induced changes to dietary plant fatty-acids (Frank 2011), diminished metabolic savings with higher ambient temperatures (Frank 2011) and decreased reproductive allocation from depleted over-winter energy stores (Williams et al. 2015). Seasonally, heat stress during the active season could reduce foraging time and mass gain before the following hibernation period (Webb et al. 1979). During hibernation, increased temperatures as well as insufficient snow cover could reduce habitat (e.g. burrow) insulation leading to frequent arousals, accelerated use of fat stores and ultimately an increased risk of mortality (e.g. in cascade golden-mantled ground squirrel *Callospermophilus saturatus*, Geiser and Kenagy 1988; in hazel dormouse, *Muscardinus avellanarius*, Pretzlaff and Dausmann 2012).

Hibernation may prolong lifespans over several timescales. Over evolutionary time, hibernation appears to have contributed to longer lifespans and slower life histories than non-hibernating species of the same size (Turbill et al. 2011); this may be due to reduced predation (Turbill et al. 2011) and to reductions in metabolic rate (Wu and Storey 2016) during hibernation. Over the past few centuries, hibernating small mammals have been less vulnerable than homeotherms to extinction, likely because many utilise torpor or hibernation during adverse conditions (Geiser and Turbill 2009). Recent work has shown that extant hibernating mammals are not more likely than non-hibernating mammals to have responded to climate changes so far (McCain and King 2014), yet ongoing deterioration in the conditions necessary for hibernation (e.g. cold temperatures) may mean hibernators will become more vulnerable to additional change (Geiser and Turbill 2009). Overall, we still lack a mechanistic understanding of the climate-induced shifts in life history traits that will help predict hibernator persistence.

Some of the best-studied hibernators, such as yellow-bellied marmots *Marmota flaviventer*, are generally experiencing increasing temperatures, declining winter snowfall, earlier snowmelt and extended growing seasons (Cordes et al. 2020). However, these trends – and species' experiences of them – vary widely year-to-year: increased variability in climatic conditions reflects another aspect of climate change (Thornton et al. 2014), making it harder for hibernators to adopt bet-hedging tactics that would help maximize maintenance, growth, reproduction and survival from one year to the next. Relationships that exist between climatic variability and hibernator life histories may further vary across latitude and elevation.

Climate studies reveal that warming is generally greater at higher than lower latitudes (Trenberth et al. 2007), amplifying latitudinal differences in phenological advancement linked to warming in both plant and animal species (Post et al. 2018). Hence, temperate and arctic hibernators could be experiencing more drastic shifts in phenology in response to warming when compared to their tropical counterparts. However, these hibernators tend to use deep burrows or caves for hibernacula, which maintain relatively constant ambient temperatures despite external fluctuations in winter temperatures. By contrast, tropical hibernators at lower latitudes tend to use poorly insulated dens, such as tree holes, and may be less buffered against high temperatures and wide fluctuations in temperature during the tropical winter (Dausmann et al. 2004; but see Blanco et al. 2013). Additionally, tropical hibernators may hibernate for shorter periods than temperate species, depending on season length and initiate extended torpor in response to a wider variety of environmental triggers (Nowack et al. 2020). Whether accelerated warming at higher latitudes has a disproportionate impact on hibernator life histories when compared to tropical counterparts remains to be assessed. Precipitation changes may also vary along elevation gradients (IPCC 2018). For example, mountain regions around the globe are experiencing shorter periods of annual snowcover, but reductions in snow depth are greater at lower than higher elevations (IPCC 2018). Based on the idiosyncratic nature of climate change across elevation, we expect shifts in hibernator performance to depend on study location (e.g. lower or higher along an elevational gradient).

The overarching goal of this review is to synthesize findings collected from studies that provide insight into the mechanisms that govern life history responses to climate change in mammalian hibernators. We specifically report the direction and significance of shifts in hibernator phenology, growth, reproduction and survival to components of climate change; identify age-, season- and sex-specific variation in life history responses, as well as sources of behavioral plasticity that may mediate those responses; and the ecological implications of directional shifts. We also identify taxonomic, geographic and condition-specific knowledge gaps in our understanding of climate-life-history links. Our aim is to help connect transdisciplinary dots, improve our understanding of life history responses to climate change in hibernators across

taxonomic groups, and ultimately provide guidance in their conservation.

Predictions: relationship between climate change and hibernator performance

Life history signature

The impact of warming on hibernating species performance may be contrasted with respect to taxonomic differences in resource selection and use (e.g. in habitat selection and diet preference). For example, bats should be generally less affected by warming temperature during hibernation because of their ability to adjust their exposure to ambient temperature during hibernation by shifting locations within caves in between bouts of torpor (Neuweiler 2000), whereas burrowing hibernators depend on their choice of hibernaculum throughout winter for survival (Goldberg and Conway 2021).

Dietary differences may also dictate hibernator-specific responses to a warming climate via the impact on the primary food source. For instance, warmer active-season temperatures may benefit insectivorous bats by increasing the activity of insect prey, while faster accumulation of growing degree days will shift the flowering and phenology of plants (Wadgymar et al. 2018) that herbivores rely on to 'match' their phenology to ensure body mass gains and growth, ultimately resulting in increased probabilities of reproduction and survival.

Although we may be limited in our ability to test these predictions given paucity of studies on these topics, we expect younger age-classes to be systematically less buffered against shifts in temperature and precipitation than older age-class, independent of the hibernating species considered, simply because of their size and lower ability to thermoregulate (Patil et al. 2013); this prediction is congruent with the demographic buffering hypothesis, which predicts that because adult survival contributes more to population growth, it should be less sensitive to environmental variation than juvenile survival (Hilde et al. 2020). Juvenile age classes may also have less of a choice in selection for their hibernacula with energetic consequences during hibernation (e.g. juvenile bats found at cave entrances (Neuweiler 2000), or juveniles squirrels found in shallow hibernacula (Young 1990)). Males and females should also respond differently to climate change because of differences in peak energy expenditure between sexes: e.g. spring breeding for temperate male hibernators, versus early summer lactation for females (Kenagy et al. 1989a). Finally, species that hibernate socially may benefit from this strategy when compared to asocial species by increasing energy efficiency during both normothermy and hibernation (Boyles et al. 2008). Group structure may also be important in improving energetic efficiency with older, larger individuals producing body heat that reduces the arousal costs for juveniles.

Seasonal signature

We expect that warmer and drier conditions should have negative effect on hibernator emergence phenology and

hibernation duration, as would shorter winters and longer growing seasons, and a positive effect on hibernator immergence. Though warmer overwinter temperatures may reduce the energetic efficiency of hibernation (Neuweiler 2000), exhausting fat reserves before spring, this may be offset by shorter winters and longer active seasons. Additionally, warmer active season temperatures should reduce the higher costs of normothermy, allowing more energy to be stored as fat or channeled into reproduction; however, very high temperatures during the active season may challenge thermoregulation of species adapted to cooler conditions (Armitage 2013), reducing activity including time spent foraging (Melcher et al. 1990). Drying trends may increase individual water stress (Sherwin et al. 2013), reduce food quality and/or quantity (Sloat et al. 2015), and loss of winter snow cover may also increase costs of hibernation in cold environments (e.g. Arctic, alpine or mountain ecosystems; Tafani et al. 2013, Rézouki et al. 2016, Sheriff et al. 2017, respectively). Therefore we expect warmer (but not extreme) temperatures, shorter winters and longer growing seasons to overall have positive effects on body condition and growth, and drier conditions to have negative effects on body condition and growth.

For reproduction, high internal body temperatures and metabolic rates are required for seasonal sexual development (males) and gestation (females) (Dausmann 2014); hence, reproduction in hibernators must take place when animals are normothermic, during the active season. Higher reproductive success should track phenological match with key resources, as mothers face less severe tradeoffs between energetic investment in offspring versus their own pre-hibernation body condition when resources are plentiful during reproduction. We hypothesized that early spring warming should lengthen growing seasons (Buermann et al. 2018), giving more time for males to become seasonally sexually mature leading to higher fertility (Komar et al. 2022). In addition, if warming leads to shorter hibernation durations, one would expect males and females to emerge in better condition, leading to a higher proportion of reproductively active individuals and larger, more successful litters.

Last, climate change should lower survival overwinter due to energetic depletion tied to a loss of snow insulation, especially at higher elevation and latitudes. Climate change should also affect active-season survival for smaller species because of increased predation risk with a longer active season. Further, because colder seasons are warming faster than warmer seasons (IPCC 2018), we expected over-winter survival to be more severely impacted than active-season survival.

Geographic signature

Given that hibernation duration and efficiency are linked to resource availability and ambient temperatures, we had several expectations for how climatic change should affect hibernator performance. Generally, we expected that warming trends at high elevations and high latitudes should extend the usually short vegetative growing seasons there, prolonging the season when activity is profitable for hibernators in

terms of body condition, growth, reproduction and survival (Ozgul et al. 2010).

Regarding phenology, we expected earlier emergence from hibernation in the spring, and later immergence into hibernation in the fall for high latitude hibernators. For hibernators at tropical latitudes that are not experiencing the same extent of warming (IPCC 2018), we expected smaller shifts in the timing of emergence and immergence from hibernation, thus likely smaller gains in body condition, reproduction or growth. However, these predictions only hold true as long as the phenological match between hibernators and their main resource remains. Warming could affect plant nutritional quality and availability over summer and fall, negating any positive impact of an elongated growing season.

Methods

Review selection process

We identified studies that addressed mammalian hibernator responses to anthropogenic climate change by conducting a standardized literature search in the ISI Web of Knowledge. Our final search took place on 5 August 2020 and identified studies published between 1950 and 2020. Searching for relevant studies with combinations of the following keywords – climat* AND hibern*, weather AND hibern* – generated a list of 717 citations (see PRISMA flow diagram presented in Fig. 1).

We qualitatively disregarded studies that addressed topics that were not in line with our review: those that reported on species that did not truly hibernate (i.e. animals that exhibit torpor bouts < 24 h, Geiser and Ruf 1995), or species that were not mammals. We further excluded studies where no statistics were reported, for which we could not find an English version, or that did not present sufficient evidence to detect a relationship between life history traits and climate or weather. We accepted experimental work if conducted in natura, but excluded studies that focused on habitat selection processes, activity budgets and physiological correlates of hibernation, as opposed to the traits of interest to our study: phenology, body mass/condition and growth, reproduction and survival.

Once a working subset of studies was identified ($n = 39$), we separated results based on the key life history traits of interest (phenology, body mass/condition and growth, reproduction and survival) and collected the following information for each entry in our dataframe: the species common name, Latin name, order, study type (qualitative, quantitative or review), ecosystem (desert, forest, grassland, mountain/alpine, rainforest, savannah, tundra or other), field site location, latitude, longitude, length of study, beginning year, end year, life history trait(s), season in which trait was measured (summer/active, winter/hibernation), age group measured (pup, yearling, adult), social/reproductive status (e.g. reproductive versus non-reproductive, subordinate versus dominant), general climatic driver(s) (i.e. drought index, global index, rain, snow, temperature), specific climatic driver(s)

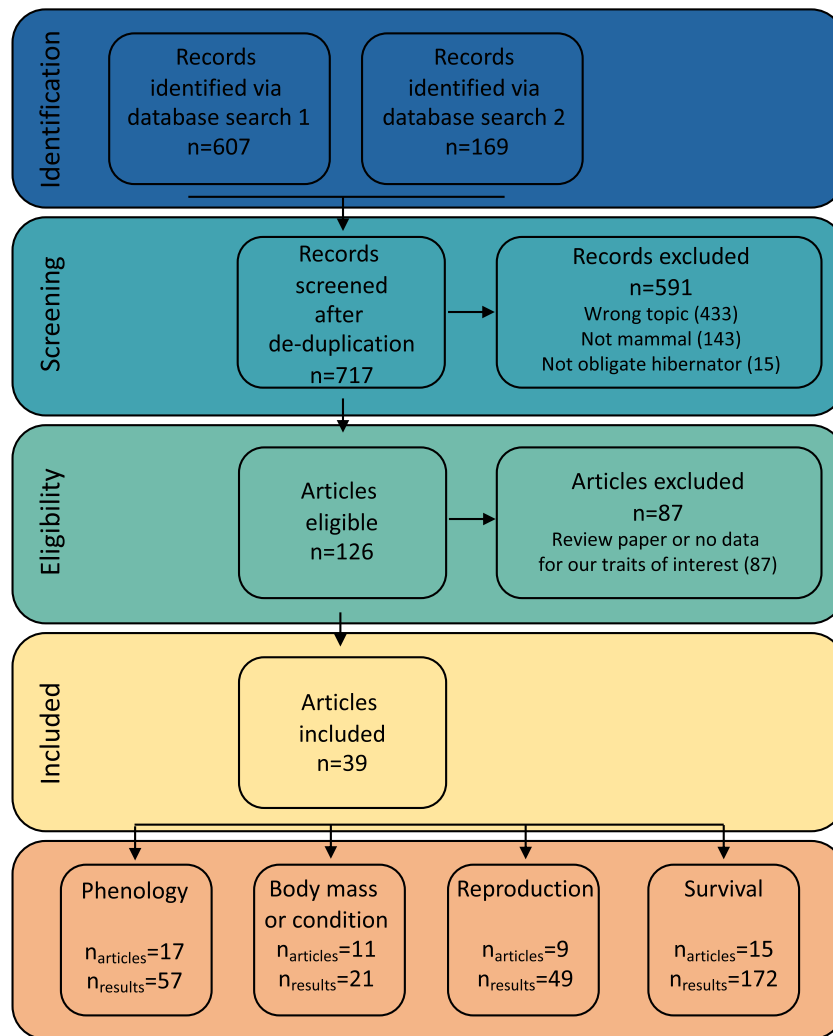


Figure 1. PRISMA flow diagram of studies identified, screened, eligible and included in this systematic review.

(e.g. July mean maximum temperature), direction of effect(s) (i.e. negative, positive, no effect), statistical method, statistics reported, sample size and citation information (Supporting information). Because studies reported a variety of weather and climate variables, we conceptually standardized the results according to four expected future climatic conditions: warmer conditions, drier conditions, a longer growing season and a shorter winter from earlier snowmelt. For instance, a positive effect of rainfall and negative effect of drought are conceptually the same result, so those would both be categorized here as negative effect of drier conditions. Each row summarized a unique result linking a specific life history trait and climatic driver(s); hence, studies with multiple results were represented multiple times in our dataframe and in our results (Fig. 2). A meta-analysis is a powerful tool that can derive meaningful conclusions from data, however, there are situations in which meta-analysis is not appropriate: when field methodologies are inconsistent, when statistical methodologies are inconsistent, and when bias may be present (e.g. difference in inference and potential for bias based on study

length and sample size). All of these conditions applied to the studies identified in our systematic review, and so precluded a formal meta-analysis. Therefore, we used binomial tests to evaluate the effects of each climate component (warmer, drier, longer growing season, shorter winter) on each life-history trait (phenology, body mass/condition and growth, reproduction, survival), comparing the number of significant results in the expected direction (positive, negative) out of total number of significant results reported. Though this approach is rudimentary, it is a first step toward organizing somewhat sparse and heterogeneous data. Note that given small sample sizes for some component-trait combinations, ‘significance’ of binomial tests should be cautiously interpreted: significant results of binomial tests likely highlight consistent patterns, but high p-values may reflect few studies yet conducted. Additionally, results are not corrected for phylogenetic similarity. In our results, we distinguish between duration of torpor (discrete bouts of lowered metabolism between periods of arousal to normothermy) versus hibernation (period from initiation of first torpor bout in fall to last torpor bout).

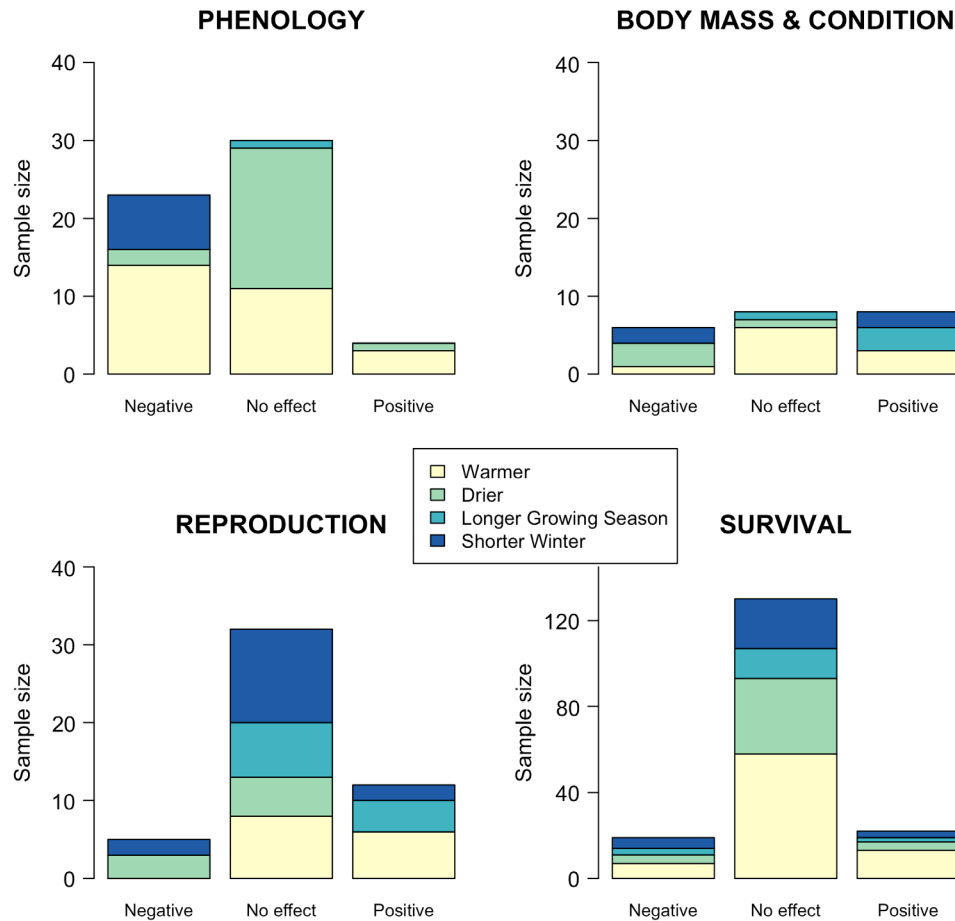


Figure 2. Direction of the effects (i.e. negative, no effect or positive) of key climatic drivers (i.e. warmer temperatures, drier conditions, longer growing seasons and shorter winters) on the life history responses (i.e. phenology, body mass/condition and growth, reproduction and survival) of hibernating species. Sample size is reported on the y-axis, and direction of the effects on the x-axis. Note the scale on the y-axis of the Survival plot differs from the other plots.

Results

Direction and significance of climate-driven shifts in hibernator life histories

Study durations ranged from 2 to 69 years, though with one re-survey design that covered a 108-year span (Eastman et al. 2012). We found no pattern of significant climate-trait outcomes by study duration: longer studies did not report a higher percentage of significant positive or negative findings out of the total number of relationships investigated (i.e. the slope parameter β_0 for the relationship between study duration and percentage of significant results = 0.002, SE = 0.005, t-value = 0.365; β_0 was not significantly different from 0, p-value = 0.720). Also, we found no pattern of significant climate-trait outcomes by decade: studies that ended more recently did not report a higher percentage of significant positive or negative findings than older studies ($\beta_0 = -0.019$, SE = 0.007, t-value = -1.596, p-value = 0.130). Of the 299 climate-trait relationships reported in the studies we reviewed, approximately half sought to determine the effects of temperature (n = 133), and another half sought the effects

of precipitation ($N_{\text{snow}} = 76$, $N_{\text{rain}} = 39$, $N_{\text{drought}} = 17$), while $N = 19$ were attributed to 'global climatic index' ('GCI') and another 15 to other drivers (Supporting information).

Phenology

We found 17 studies describing 57 phenological responses of 12 hibernating species ($N_{\text{Rodentia}} = 7$, $N_{\text{Chiroptera}} = 3$, $N_{\text{Carnivora}} = 2$) to climate variables (Supporting information; Fig. 2a). Though more rodent and bat species than carnivore species were studied, phenology results were disproportionately from carnivores (Supporting information). Study duration ranged from 2 to 65 years, with results focused on hibernation duration (n = 8), emergence (n = 34) and immergence (n = 15, Supporting information).

Generally, climatic shifts were associated with negative or no effect on spring phenology, meaning earlier dates of emergence from hibernation in spring, shorter hibernation duration or no change (Fig. 2a). Warmer temperatures and shorter winters had reliably negative effects on hibernation emergence phenology, but studies of drier conditions were few (Table 1). A longer growing season, measured as last date of spring frost, had no effect on hibernation emergence in

Table 1. Binomial tests for direction of significant effects of individual climate components on life history traits. Combined number of positive and negative effects for each trait are presented in italics; statistically significant binomial results are presented in bold.

Trait	Climate component	Relationship direction expected	Number significant results in direction expected	Total number of significant results	Probability of success	95% confidence interval	p-value
Phenology							
Hibernation duration	Higher temperature	Negative	2	2 (2 −, 0 +)	1.0	0.16–1.0	0.5
	Less precipitation	Negative	0	0 (0 −, 0 +)	0.0	NA	NA
	<i>Overall</i>	<i>Negative</i>	2	2 (2 −, 0 +)	1.0	0.16–1.0	0.5
Hibernation emergence	Higher temperature	Negative	10	10 (10 −, 0 +)	1.0	0.69–1.0	0.002**
	Less precipitation	Negative	2	3 (2 −, 1 +)	0.67	0.09–0.99	1
	Longer growing season	Negative	0	0 (0 −, 0 +)	0.0	NA	NA
	Shorter winter	Negative	7	7 (7 −, 0 +)	1.0	0.59–1.0	0.02*
	<i>Overall</i>	<i>Negative</i>	19	20 (19 −, 1 +)	0.95	0.75–1.0	< 0.001**
Hibernation immergence	Higher temperature	Positive	3	4 (1 −, 3 +)	0.75	0.19–0.99	0.625
	Less precipitation	Positive	0	0 (0 −, 0 +)	0.0	NA	NA
	<i>Overall</i>	<i>Positive</i>	3	4 (1 −, 3 +)	0.75	0.19–0.99	0.625
Body mass/condition							
	Higher temperature	Positive	3	4 (1 −, 3 +)	0.75	0.19–0.99	0.625
	Less precipitation	Negative	3	3 (3 −, 0 +)	1.0	0.29–1.0	0.25
	Longer growing season	Positive	3	3 (0 −, 3 +)	1.0	0.29–1.0	0.25
	Shorter winter	Positive	2	4 (2 −, 2 +)	0.5	0.07–0.93	1.0
	<i>Overall</i>		11	14	0.79	0.49–0.95	0.06
Reproduction							
	Higher temperature	Positive	6	6 (0 −, 6 +)	1.0	0.54–1.0	0.03*
	Less precipitation	Negative	3	3 (3 −, 0 +)	1.0	0.29–1.0	0.25
	Longer growing season	Positive	4	4 (0 −, 4 +)	1	0.40–1.0	0.125
	Shorter winter	Positive	2	4 (2 −, 2 +)	0.5	0.07–0.93	1.0
	<i>Overall</i>		15	17	0.88	0.64–0.99	0.002**
Survival							
	Higher temperature	Positive	13	20 (7 −, 13 +)	0.65	0.41–0.85	0.26
	Less precipitation	Negative	4	8 (4 −, 4 +)	0.5	0.16–0.84	1.0
	Longer growing season	Positive	2	5 (3 −, 2 +)	0.4	0.05–0.85	1.0
	Shorter winter	Positive	3	8 (5 −, 3 +)	0.375	0.09–0.76	0.73
	<i>Overall</i>		22	41	0.54	0.37–0.69	0.76

* $p \leq 0.05$, ** $p \leq 0.01$

the one study where it was investigated (Miller et al. 2017). Among the few positive effects on phenology were warmer fall temperatures delaying hibernation immergence in black bears *Ursus americanus* (Johnson et al. 2018) and brown bears *Ursus arctos* (Evans et al. 2016, Delgado et al. 2018).

In rodents, warmer temperatures had a negative effect on hibernation emergence ($n=5$, Fig. 2a and Supporting information) and on hibernation duration ($n=1$, Fig. 2a). Specifically, spring temperatures were the main driver of earlier phenology in studies of edible dormice (Adamík and Král 2008), common hamsters *Cricetus cricetus*, Columbian ground squirrels *Urocitellus columbianus* (Michener 1977, Lane et al. 2012), Richardson's ground squirrels *Urocitellus richardsonii* (Michener 1977) and yellow-bellied marmots *Marmota flaviventris* (Edic et al. 2020).

In bats, daily minimum temperature during torpor negatively affected hibernation emergence, immergence and duration ($n=3$, Fig. 2a, 3b and Supporting information) in both temperate (Hodgson's bat, *Myotis formosus*, Kim et al. 2013)

and tropical species (eastern long-eared bats *Nyctophilus bifax*, Stawski and Geiser 2012). As temperatures across the tropics are expected to continue to rise (IPCC 2014), affecting energy use and foraging requirements, we may expect widespread disruptions to torpor in tropical hibernators (Stawski and Geiser 2012). However, the absence of additional studies on tropical hibernators points to an obvious gap in the literature, which in light of climate change is concerning for their conservation (Fig. 3c and Supporting information).

Growth, body mass and condition

We found 11 studies describing 21 body condition or growth responses of 11 hibernating species ($N_{\text{Rodentia}}=8$, $N_{\text{Chiroptera}}=2$, $N_{\text{Eulipotyphla}}=1$) to climate variables (Fig. 2b); results were disproportionately from rodent species (Supporting information). Study duration ranged from 2 to 54 years.

Reported effects were both positive (increasing body condition or growth) and negative (decreasing body condition or growth), though there were too few significant results to draw

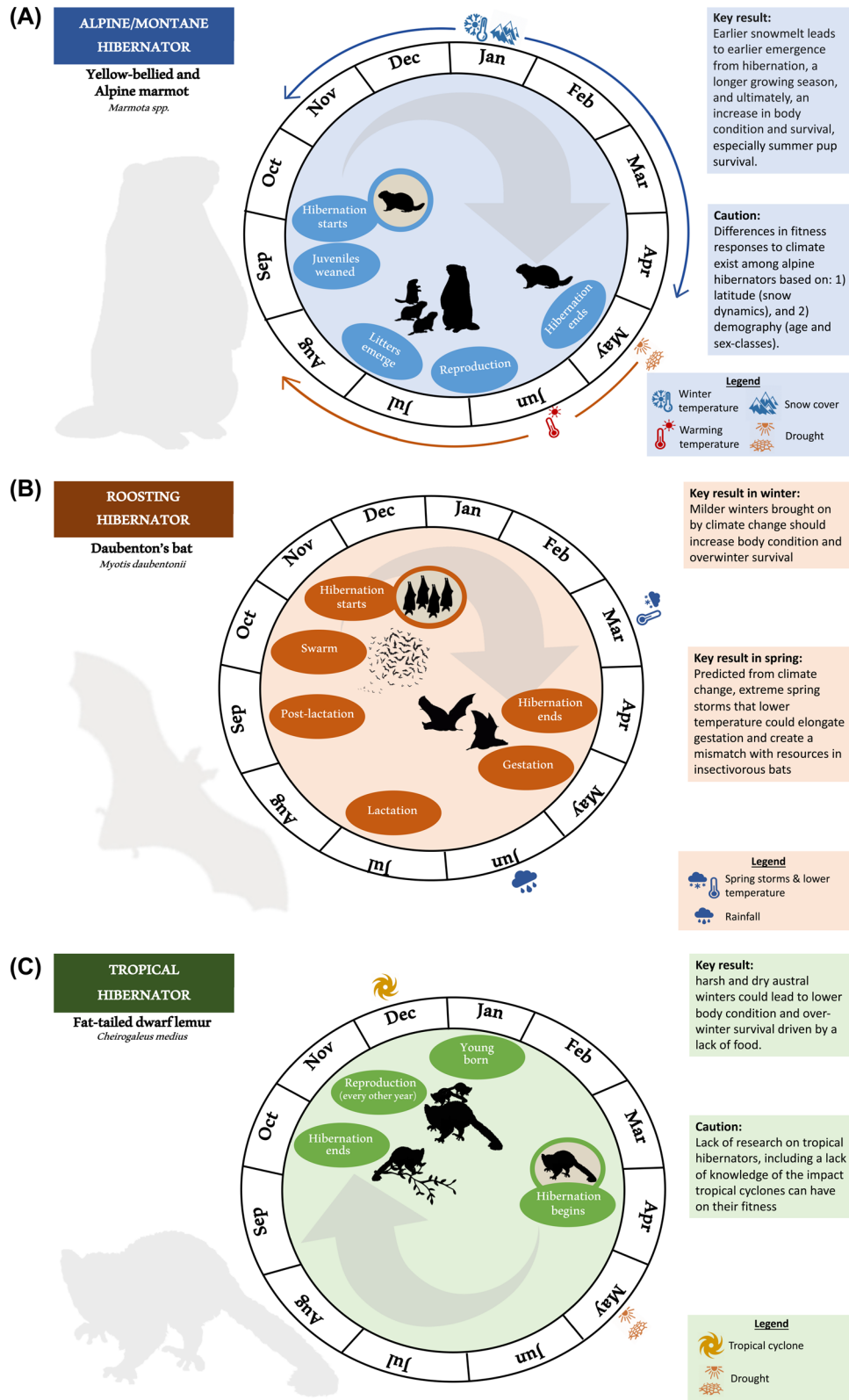


Figure 3. Realized effects of climate change on hibernator life histories across three generic life cycles, as well as their potential response to current and future climate change: (a) the yellow-bellied or alpine marmot, (b) Daubenton's bat and (c) the fat-tailed dwarf lemur.

conclusions from the sign tests for any single component of climate (Table 1). Warmer conditions generally had no effect, but were associated with better body condition for a few species. Western hedgehogs *Erinaceus europaeus* in Ireland weighed more overall and lost less mass over the hibernation period than those in the UK and Denmark, perhaps due to the milder winters in Ireland (Haigh 2012). Warmer spring temperatures increased body condition in several species of bats (pallid bats, *Antrozous pallidus*, Lewis 1993; greater mouse-eared bats, *Myotis myotis*, Zahn et al. 2007). For insectivorous bats in particular, warmer active-season temperatures may positively affect body condition in two ways – by reducing the energetic costs of homeothermy, and by increasing the activity of insect prey (Fig. 2b).

Snow cover during winter may affect the body condition of subterranean hibernating species by its duration (affecting the length of hibernation) and its depth (affecting its insulating properties). Drier conditions had largely negative effects, while effects of shorter winters were mixed (Table 1). Male Townsend's ground squirrels (*Urocitellus townsendii*, Van Horne 1997) and female arctic ground squirrels *Urocitellus paryii* experiencing longer snow cover were in better body condition than those experiencing a shorter winter (Sheriff et al. 2017). However, arctic ground squirrels also had higher glucocorticoid levels, suggesting longer snow cover is physiologically more stressful (Sheriff et al. 2017). Only one study quantified the effect of snow depth on body mass/condition, and found thinner snowpack in the French Alps was associated with lower body condition of adult female Alpine marmots *Marmota marmota* over the past decades (Tafani et al. 2013). For Townsend's ground squirrels, drier summer conditions also reduced body mass, likely due to poorer vegetation quality and quantity (Van Horne et al. 1997).

Across multiple species, active season length appeared to have a positive effect on growth. Larger adult body sizes of Belding's ground squirrels *Urocitellus beldingi* and golden-mantled ground squirrels *Callospermophilus lateralis* in contemporary (2008) versus historical (1902–1950) specimens were attributed to longer growing seasons and availability of nutritious forage with earlier snowmelt dates over time (Eastman et al. 2012). However, facultatively-hibernating California ground squirrels *Otospermophilus beecheyi* at lower elevations did not show any change in size over time (Eastman et al. 2012). Similarly, longer growing seasons were sometimes associated with more rapid growth in juvenile yellow-bellied marmots (Ozgul et al. 2010; but see Paniw et al. 2020), and higher body condition entering hibernation in greater mouse-eared bats (Zahn et al. 2007).

Reproduction

We found 9 studies describing 49 reproductive responses of 8 hibernating species ($N_{\text{Rodentia}}=7$, $N_{\text{Chiroptera}}=1$) to climate variables (Fig. 2c); results were nearly all from rodents (Supporting information). Study duration ranged from 2 to 40 years. The majority of climate variables tested had no effect on reproduction, but some effects were positive (Fig. 2c). Warmer conditions significantly improved reproductive output (Table 1),

and longer growing seasons often did. In common hamsters, females doubled their reproductive output following a warmer shorter winter, compared to a year with longer spring snow-cover (Hufnagl et al. 2011); in yellow-bellied marmots, a higher percentage of females reproducing in years with longer growing seasons (Schwartz and Armitage 2005). In many rodent hibernators, males must maintain high normothermic body temperatures for several weeks to achieve sexual maturity in the spring (e.g. ground squirrels, Barnes et al. 1986). The energetic costs of normothermy depend on the difference between body temperature and ambient temperature: energetic costs increase with lower ambient temperatures and hence larger differences in body versus ambient temperatures. With warmer ambient spring temperatures, more males will likely be able to maintain the high temperatures required for testicular development and spermatogenesis. Indeed, in one result from edible dormice more sexually active males were associated with more litters born, suggesting that more sexually mature males in years with warmer temperatures will contribute to population growth (Fietz et al. 2004).

Drier conditions often reduced reproduction, either due to increased metabolic costs under thinner snowpack over winter (Tafani et al. 2013), or reduced food availability with less summer rain (Van Horne et al. 1997, Schwartz and Armitage 2005). However, later snow melt brought about by delayed spring snow storms led to a decrease in litter size in Columbian ground squirrels *Urocitellus columbianus* (Lane et al. 2012). The increased frequency of spring snow storms at higher latitudes predicted by climate change (Gergel et al. 2017) may lead to a mismatch between emergence from hibernation and food availability in rodents (Dobson et al. 2016), with spring and summer becoming less distinct than in the past.

Survival

We found 15 studies describing 172 survival responses of 12 hibernating species ($N_{\text{Rodentia}}=6$, $N_{\text{Chiroptera}}=6$) to climate variables, along with a review paper that investigated the response of 15 species of hibernating rodents to climate change (Fig. 2d); results were disproportionately from rodent species (Supporting information). Because 3 studies focused on the same long-term study of yellow-bellied marmots in Colorado, we excluded the shortest study to reduce pseudo-replication. Study duration ranged from 5 to 40 years.

Overall, the climate components tested had no consistent effects on hibernator survival (Table 1), but both positive and negative effects were found for some species. Warmer conditions largely had no effect on survival, but were positive for Daubenton's bats (*Myotis daubentonii*, Culina et al. 2017, Fig. 3b), Alpine marmots (Farand et al. 2002, Rézouki et al. 2016) and yellow-bellied marmots (Cordes et al. 2020, Paniw et al. 2020); and negative for juvenile Leisler's bats (*Nyctalis leisleri*, Schorcht et al. 2009) and many species of hibernating rodents (Turbill and Prior 2016). Effects of shorter winters were more negative than positive (Fig. 2d), perhaps as an indirect effect of lower predation rates during hibernation (Turbill et al. 2011). In fall, an increase in the intensity of frost led to a decrease in adult survival for alpine

marmots, suggesting that colder temperatures at the onset of hibernation could set high energetic costs over winter and lead to decreased survival in mature animals (Farand et al. 2002).

Of the results reported, all but 3 provided age-specific survival estimates with respect to weather and climatic variables, indicating a shared understanding that survival is expected to vary widely with age in hibernating species, especially between juvenile and adult age classes. Accordingly, results were often age- and season-specific. For example, warmer winter temperatures decreased over-winter survival for yearling and adult Uinta ground squirrels *Urocitellus armatus* (Falvo et al. 2019). However, warmer winter temperatures conferred a survival benefit to juveniles (Falvo et al. 2019). Juveniles have a larger surface-to-volume ratio than yearling and adults, likely forcing them to expend more energy while hibernating (Körtner and Geiser 2000, Sherman and Runge 2002); this could explain why they tend to survive over winter at a higher rate when ambient winter temperatures are above freezing.

Collectively, these results support the importance of seasonality (i.e. season-specific survival estimation) and demography (i.e. age-specific and sex-specific estimates) in explaining variability in the relationships that exist between warming temperatures, drier conditions and life history traits in hibernators.

Discussion

Shifts in hibernator performance traits in light of climate change

The impacts of climate components on hibernating species varied by life history trait. Warming trends appeared to yield consistently positive effects on hibernator reproduction, increasing both fertility (Fietz et al. 2004, Paniw 2020) and reproductive output (Schwanz 2006, Hufnagl et al. 2011, Fietz et al. 2020). However, drying trends that reduce winter snowpack may erode female body condition and subsequent reproductive success (Tafani et al. 2013). Consistent with other reviews (Boutin and Lane 2014), warming trends also reliably advanced hibernation ending in spring and sometimes delayed hibernation onset in fall. By contrast, survival showed season-, species- and age-specific responses instead of consistent directional change. Responses of growth and body condition to changing climatic conditions have received the least research attention so far, and more work is needed to be able to predict both general trends and species- and age-specific responses.

Our approach to analyze these heterogeneous data had both strengths and weaknesses. The strength of a systematic review is to reduce bias in identifying relevant research; however, it cannot solve potential issues of publication bias (i.e. bias against publishing null results) and the volume of candidate studies identified took substantial effort to screen and synthesize. To attempt to numerically synthesize these disparate data, we applied a sign test to evaluate whether hibernator life history responses to climate change components were

(a) consistent, and (b) in the direction expected. Weaknesses of this approach are that it ignores the magnitude of effects from individual studies, does not weight study results by sample size, and assumes independence between studies. In short, it is not a meta-analysis: 'significant' results should indicate consistent effects, but others should be interpreted cautiously. However, this approach did highlight the climate component-life history trait combinations with the fewest published results, which could be considered priorities for future study. We discuss some of these and other research gaps revealed in the systematic review below.

Age-specific responses

Reproduction and subsequent juvenile independence is generally timed with peak food abundance in hibernators (Walker 1968). Phenological mismatches occur when peak food resource abundance is offset from peak resource needs. Because resource needs vary with age and reproductive stage, phenological mismatches brought about by climate change may not impact all individuals within a population of hibernators equally. Newly-weaned juveniles have the least amount of time to gain body mass before hibernation, and they may also expend more energy while hibernating (Körtner and Geiser 2000, Sherman and Runge 2002), making them more susceptible to phenological mismatches than older age classes (Miller-Rushing et al. 2010). Hotter and drier summers that cause grasses to senesce earlier (Walker 1968), and mid-summer declines in floral abundance (Aldridge et al. 2011), could disproportionately affect juvenile growth and pre-hibernation fattening.

These phenological shifts or reductions in food availability translate into reduced juvenile overwinter survival. Indeed, juvenile Columbian ground squirrels (*Urocitellus columbianus*; Dobson et al. 2016) that weaned later had lower overwinter survival compared to early weaned juveniles possibly due to decreased access to quality forage later in warmer and drier summers (Neuhaus 2000). A longer growing season could still benefit juveniles if their emergence is timed well with high quality forage (Zahn et al. 2007), but could negatively impact juveniles via increased exposure to predators if juveniles are more susceptible to predation compared to adults (Cordes et al. 2020).

In species where juveniles hibernate alone, they may select less-optimal hibernacula locations (Shaw 1926), or have less access to quality (deep) hibernacula because adults already occupy those, leading to reduced over-winter survival rates. Although it is technically challenging to study hibernaculum selection and thermal conditions in shaping over-winter survival chances, studies conducted below-ground, in natura, over more than one winter (Buck and Barnes 1999b), would help explain age-specific differences in performance among species that hibernate in different parts of the world.

Sex-specific responses

Peak energy expenditure for males tends to arise during the mating period either in spring (for sciurids, Buck and Barnes 1999a) or in fall (for bats, Encarnação et al. 2006), but for

females occurs during lactation, generally in early summer (Kenagy et al. 1989b, Kurta et al. 1989). One would thus predict the impacts of climate change on hibernator performance to follow different seasonal patterns in males and females. In the edible dormouse, observed differences in the survival rates between females and males was relatively small, however male survival was slightly lower than that of females: compared to females, males tend to be more active and have larger home ranges, and hence may face increased predation risk (Lebl et al. 2011).

In locales where climate change favors an expansion of the growing season and a phenological match with resources, these sex-specific differences may be minimized, and vice versa where hibernators suffer a phenological mismatch with key resources, sex-specific differences may be exacerbated. Arctic ground squirrels in northern Alaska showed sex-dependent plasticity in the physiology and phenology of hibernation in response to a series of late spring snowstorms that resulted in the latest snowmelt on record (Williams et al. 2017). Female reproductive activity was delayed by more than two weeks, while reproductive males did not extend or re-enter hibernation, likely because gonadal growth and testosterone production prevented a return to torpor. This supports the idea of sex-specific responses to climatic stressors, leading to a phenological mismatch between the sexes (Williams et al. 2017).

Behavioral mediation of climate effects

Behavioral changes in winter micro-site selection (Boyles et al. 2007), food caching (French 2000) and nest use (Marrant and Petit 2011) may allow some species to adapt to changes in ambient temperatures during hibernation. We know that bats are able to adjust their exposure to ambient temperature during hibernation by shifting locations within caves in between bouts of torpor (Neuweiler 2000), and appear to do so based on their own energy availability (Boyles et al. 2007). During winter, cave entrances are colder, and hence provide the highest energetic savings for bats; these locations are often chosen by juvenile bats, with lower fat reserves, who cannot afford to overwinter in the deepest part of the caves where ambient temperatures are slightly warmer (Neuweiler 2000). However, temperature fluctuations are also more extreme near cave entrances, and bats arousing to shift locations is metabolically expensive (Neuweiler 2000). With warming winter temperatures, juveniles may require more fat reserves or an increase in foraging between bouts of torpor.

We know far less about the ability of burrowing hibernators (i.e. most ground-dwelling squirrels) to behaviorally thermoregulate within hibernacula, or indeed much about hibernaculum structure or conditions for most species. Increased soil temperatures are expected to reduce the metabolic efficiency of hibernation and increase energetically-expensive arousals, reducing spring body condition (Buck and Barnes 2000); but some studies have found lower-than-projected body mass declines (Németh et al. 2009, Németh 2012). Males of some, but not all, species of smaller hibernating sciurids cache seeds to fuel early spring periods of normothermy (Williams et al. 2014). Yet, it is unclear whether

females and juveniles could or would acquire this behavior if more frequent, metabolically-expensive arousals are necessary in response to soil or ambient temperatures.

In arboreal hibernators, selection of hibernacula may be an important but flexible component of overwinter survival. For example, Malgasy fat-tailed dwarf lemurs prefer hibernacula in larger tree species, which confer better insulation than active season nests (Dausmann 2012). Dormice in temperate regions construct insulated winter nests in trees (Walhovd 1976), as do pygmy-possums in Australia (Namekata and Geiser 2009).

Social structure

Group size and composition could further affect fitness in social species that hibernate in groups, such as marmots (Armitage 2017), bats (Willis and Brigham 2007) and pygmy-possums (Namekata and Geiser 2009). Social thermoregulation has been found to increase energy efficiency both during normothermy (Namekata and Geiser 2009) and hibernation (Willis and Brigham 2007, Armitage 2017). The presence of older group members seems to particularly reduce the overwinter mortality of juveniles (Arnold 1990, Patil et al. 2013), perhaps by producing body heat that reduces the arousal costs for juveniles with lower fat reserves. However, social thermoregulation may only partially offset the energetic costs of hibernation (Arnold 1988), as winter weather conditions have more influence on survival of all age classes than group composition (Patil et al. 2013).

Seasonal responses to climate change

Changes to winter (hibernating) versus summer (active-season) climatic conditions may be the key to explaining individual gains and losses for particular phenotypes (e.g. young versus adult, male versus female). In the edible dormouse for instance, adult survival remained extremely high over winter, suggesting that these populations did not run out of energetic reserves while hibernating (Lebl et al. 2011); this result is shared by a number of other rodent studies (Neuhaus and Pelletier 2001, Schaub and Vaterlaus-Schlegel 2001, Meaney et al. 2003, Bryant and Page 2005). An obvious reason for higher survival rates during hibernation than over the active season is that the hibernaculum keeps animals safe from predators; indeed, in warming climates overall survival may decline as the active season lengthens, accompanied by a higher predation rate (Turbill et al. 2011, Turbill and Prior 2016). In the Uinta ground squirrel, however, pups experienced higher over-winter survival when temperatures were warmer during hibernation, while older age classes suffered decreased over-winter survival rates (Falvo et al. 2019). Although metabolic costs decrease with decreasing temperature and increased snow insulation in the hibernacula, arousal costs increase with decreasing temperature. This result suggests this trade-off is experienced differently by immature and mature individuals for some hibernating species (Falvo et al. 2019), which may be tempered by climate change as winters and springs continue to warm at higher elevations.

Snow cover conditions during winter can affect hibernation physiology and body condition at emergence, and duration of the active season and precipitation can alter breeding phenology, reproductive success and over-winter survival of hibernating rodents (Morton and Sherman 1978, Lane et al. 2012, Bieber et al. 2014, Dobson et al. 2016). Climate change is expected to reduce winter snow cover, which has led to reduced litter size, reduced reproductive frequency and decreased survival for multiple species (Van Vuren and Armitage 1991, Patil et al. 2013). Higher burrow temperatures are associated with shorter hibernation duration (early emergence) and lower survival due to a longer active season when animals have higher predation risk (Turbill and Prior 2016). Climate change is also shifting the timing of snow fall (more in spring; Gergel et al. 2017); a late snowfall is associated with delayed phenology and lower fitness at higher latitudes (Dobson et al. 2016).

At high elevation sites (e.g. the Rocky Mountain Biological Station in Gothic, CO), winter snowpack has declined and dates of snowmelt have advanced over the past 80 years (Wadgymar et al. 2018). Early snowmelt is associated with decreased primary productivity (Sloat et al. 2015), frost damage to plants (Inouye 2008, CaraDonna and Bain 2016) and plant population declines due to lower reproduction (Campbell 2019) and survival (Iler et al. 2019). Declines in forb abundance and reproduction are both likely to affect herbivorous hibernators, which rely on vegetative structures (e.g. leaves) and reproductive structures (flowers, seeds) for food in early and late season, respectively. Fatty acids found in seeds are crucial to efficient hibernation (Frank 2011), so declines in seed set with earlier snowmelt and drought conditions (Campbell 2019) are particularly worrying.

On the other hand, increased temperature could lead to an earlier snowmelt in spring and an earlier arousal from hibernation, reducing total energetic costs of hibernation (amount of stored fat necessary) and ultimately increasing survival. Additionally, earlier snowmelt lengthens the active season, with potential benefits for juveniles whose growth is time-constrained at high elevations: again in yellow-bellied marmots, a decrease of total snow led to an increase in juvenile (pup) summer-survival (Cordes et al. 2020). Yet, warmer summer temperatures may not always be as beneficial: while summer survival generally increased for adults and juveniles with increased temperatures, over-winter survival of both adults and juveniles declined following warmer and drier summers (Cordes et al. 2020).

Summer temperatures are expected to increase in many parts of the world (IPCC 2018) which may alter plant phenology and composition, resulting in a mismatch with the phenology of herbivorous and omnivorous hibernators (Lane et al. 2012). Also, rising temperatures may impact the amount of time available in the day when individuals can forage, due to increased risk of heat stress (Vispo and Bakken 1993, Sharpe and Van Horne 1999). Reduced foraging times may lead to either lower pre-hibernation body mass or a prolonged active season with negative impacts on overwinter

survival. Longer term warming and drying trends may allow montane and alpine ecosystems to be invaded by shrubby vegetation (Reisinger et al. 2014), reducing the nutritious, forb-dominated vegetation communities many hibernating species depend on. We did not find evidence of reduced pre-hibernation condition in the studies we reviewed, but the amount of warming experienced in the past few decades over which studies were conducted may not predict a future tipping point under extremely warm conditions (e.g. +3°C by 2090, Meehl et al. 2007).

Geographic signature: latitudinal and elevational differences in hibernator performance

Although our review indicated that earlier snowmelt and warmer spring temperatures led to earlier arousal from hibernation, the consequences of such trends on other life history components can vary based on location (i.e. latitude, elevation). For instance, in yellow-bellied marmots, years with earlier snowmelt led to an earlier emergence from hibernation and a longer growing season, resulting in an increase in over-winter survival and reproduction (Fig. 3a) (Van Vuren and Armitage 1991, Ozgul et al. 2010). In Alpine marmots however, earlier snowmelt also led to earlier emergence, but the loss of winter snow cover resulted in a decrease in both litter size and juvenile survival (Tafari et al. 2013, Rézouki et al. 2016). Thinner snow cover in extremely cold environments (e.g. French Alps, Rocky Mountains) can force marmots to catabolize their fat reserves faster than under the insulation of a deeper snowpack (Tafari et al. 2013), outweighing the benefits of a longer active season. Collectively, these results suggest latitudinal differences in snow dynamics and phenology that can scale up to affect body condition and growth in opposing ways for mammalian hibernators that are found either close to (i.e. the French Alps) or above (i.e. Alaska) the 45th parallel north versus below (i.e. Colorado Rocky Mountains).

Small mammals are typically associated with fast life-histories and multiple breeding events per year. However, small mammals at higher latitudes and higher elevations have a short breeding season (Gaillard et al. 1989) and hibernate for a substantial portion of their annual cycle, allowing animals to live longer but leading to fewer litters per year (Bieber et al. 2012). The anticipated shortening of hibernation periods with warming conditions may accelerate these slower life histories, shifting populations to a more rapid pace of life. Elevational comparisons can quantify intraspecific plasticity in life history traits such as age at first reproduction and ovulation rates (Bronson 1979), and would be usefully applied to a larger number of species. Species with faster life histories (high rates of reproduction and short life cycles) are expected to be less vulnerable to changing climates (Williams et al. 2015), but whether high-latitude and high-elevation hibernators will be able to adapt within the timescale of anticipated change remains an open question. Hibernating bats are particularly long-lived for their body size, with accompanying low offspring production (Reusch et al. 2019). As population

dynamics of long-lived hibernators are particularly driven by changes in adult mortality (Fleischer et al. 2017, Paniw et al. 2020), increases in overwinter mortality with shorter hibernation periods is concerning for population persistence in warming climates.

Several ground squirrel species at low elevations and latitudes do not use winter hibernation, but instead remain active and use shorter bouts of torpor (e.g. California ground squirrel, Dobson and Davis 1986). Species currently at higher elevations and (or) latitudes may shift to this pattern in future decades. Both black bears and brown bears in particular have been found to reduce hibernation length in response to warming falls and springs. For example, a study of black bears in Colorado observed that a 1°C increase in the winter minimum temperature was associated with a 6-day reduction in hibernation (Johnson et al. 2018). Warmer falls also postponed hibernation immergence in brown bears *Ursus arctos* (Evans et al. 2016). Yet, both studies are considerably limited in their inference, spanning only 3–5 winters.

While hibernation periods may shorten with warming trends that reduce the duration of snow cover, hibernation is unlikely to disappear for all groups. For example, woodchucks *Marmota monax* at lower latitudes in eastern North America hibernate for approximately half the time than woodchucks at higher latitudes, despite little to no snow cover (Zervanos et al. 2010). Indeed, even in mild climates, some species like echidnas hibernate facultatively, likely as an individual response to energy status (Grigg et al. 2004). Hibernators can also shift to multi-day bouts of torpor, as found in desert hedgehogs *Paraechinus aethiopicus* (Boyles et al. 2017).

Knowledge gaps and conservation implications

Temporal gaps

Though we would expect climate impacts to be most noticeable in recent decades, as temperature and precipitation changes are intensifying (Vasseur et al. 2014, Pendergrass et al. 2017), this expectation was not borne out in the studies reviewed. Our inference is limited by a number of factors such as short-time series; variability in statistical methods employed among selected studies; temporal autocorrelation; and wide variability in the reporting of results (Brown et al. 2011). However, we dissected each of the selected papers in an effort to include statistically non-significant results (which were rarely highlighted), and excluded findings that were not quantitatively evaluated. Yet, latitudinal, elevational and longitudinal variability across studies, combined with small sample size, may still limit our ability to illuminate the relationships that exist between hibernator performance and climate change.

This review highlights the need for more longitudinal studies of individuals that span multiple decades, particularly over the coming decades in which climate change is expected to intensify. Long-term studies are not only key to addressing exciting questions and providing novel insights into the ecology and evolution of life histories (Clutton-Brock and Sheldon 2010), but are also essential to informing conservation policies that may help predict and mitigate

the negative impacts of climate change (e.g. warming temperatures, increased frequency of extreme events, increased drought frequency) on plant and animal species, and hibernators in particular.

Taxonomic and geographic gaps

Our results are highly biased towards small mammal hibernators in the alpine/mountain ecosystems of both Europe and North America (Fig. 4). The average latitude of all hibernating mammals listed by Ruf and Geiser (2015) is 21.2°N, but the average latitude in our review was 42.7°N. Further, our review covers only 4 of the 11 orders of mammalian hibernators (Ruf and Geiser 2015), namely rodents and bats (Fig. 4). While the majority of mammalian hibernating species do fall in these two orders, we have virtually no long-term climate and demographic data on key representatives of mammalian diversity such as marsupials, tenrecs and elephant shrews.

For example, we do not have data from either of the two known hibernating species from South America: the dwarf-armadillo ('pichi', *Zaedyus pichi*, Superina and Abba 2014) or the high-elevation, 'living fossil' Monito del monte (*Dromiciops gliroides*, Bozinovic et al. 2004). IPCC predictions for South America include increased temperatures and drying trends (IPCC 2014), which could affect food availability for the grassland-dwelling pichi and the Chilean forest Monito. Across the African continent, similar predictions for increased temperatures and drying (Niang et al. 2014) could also affect the prey availability of predominantly insectivorous golden mole, elephant shrews (Mzilikazi and Lovegrove 2004) and tenrecs (Stephenson et al. 2019), as well as their habitat and home ranges (Stephenson et al. 2019). In Australia, Reisinger et al. (2014) predicted rising temperatures and rising snow lines will drive the loss of montane ecosystems, which would likely doom the critically endangered mountain pygmy-possum (*Burramys parvus*, IUCN 2018).

Climate change metric gaps

More research on drought conditions – particularly in relation to resource availability – would help inform hibernator susceptibility to increased drying trends expected to intensify throughout much of the globe (IPCC 2014). This is timely, as climate change creates warmer, drier conditions, increased drought that drive longer fire seasons. In both the Northern and Southern Hemispheres, combined warming and drying trends have triggered wildfires of unprecedented scale, 2019–2020 setting unfortunate records in both North America and Australia.

Fires in western North America and southeastern Australia have burned through areas that are hotspots for mammalian hibernators (Fig. 4), yet we know little about resilience to fires of this magnitude for most wildlife species that do not have the option to disperse (but see Nowack et al. 2016, and Geiser et al. 2018 for an extensive review). Historically, wild-fire seasons have coincided with the active seasons of hibernators in North America and Australia, as fire conditions peak in late summer. As fire seasons lengthen into fall with

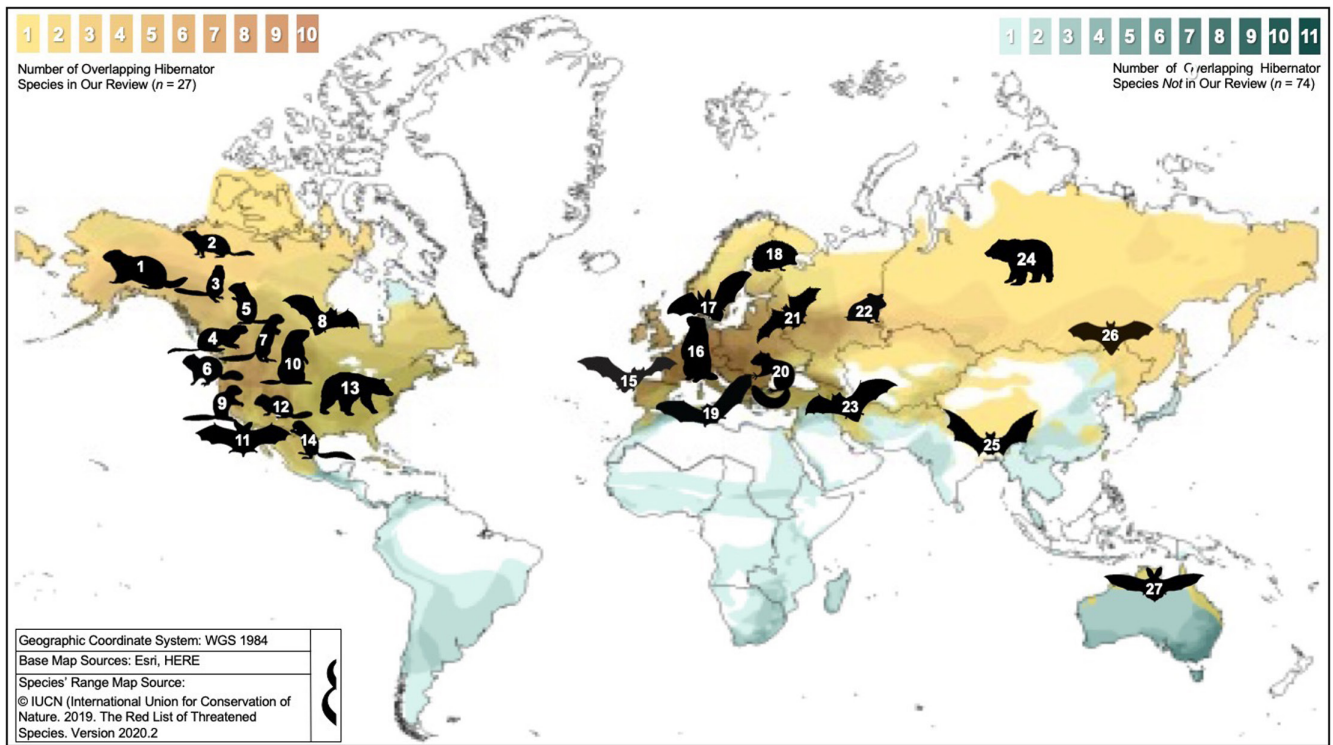


Figure 4. Global map of mammalian hibernator ranges, indicating spatial ‘hotspots’ of hibernator overlap. Icons indicate species included in this review. Warm colors indicate ranges of species included in the review; cool colors indicate ranges of species not included. 1) hoary marmot (*Marmota caligata*), 2) Arctic ground squirrel (*Urocitellus parryii*), 3) Richardson’s ground squirrel (*Urocitellus richardsonii*), 4) Townsend’s ground squirrel (*Urocitellus townsendii*), 5) Columbian ground squirrel (*Urocitellus columbianus*), 6) Belding’s ground squirrel (*Urocitellus beldingi*), 7) golden-mantled ground squirrel (*Callospermophilus lateralis*), 8) little brown bat (*Myotis lucifugus*), 9) California ground squirrel (*Otospermophilus beecheyi*), 10) yellow-bellied marmot (*Marmota flaviventris*), 11) pallid bat (*Antrozous pallidus*), 12) Uinta ground squirrel (*Urocitellus armatus*), 13) American black bear (*Ursus americanus*), 14) Mexican ground squirrel (*Ictidomys mexicanus*), 15) Leisler’s bat (*Nyctalus leisleri*), 16) Alpine marmot (*Marmota marmota*), 17) brown long-eared bat (*Plecotus auritus*), 18) western European hedgehog (*Erinaceus europaeus*), 19) greater mouse-eared bat (*Myotis myotis*), 20) edible (fat) dormouse (*Glis glis*), 21) Natterer’s bat (*Myotis nattereri*), 22) common (black-bellied) hamster (*Cricetus cricetus*), 23) common pipistrelle bat (*Pipistrellus pipistrellus*), 24) brown bear (*Ursus arctos*), 25) Hodgson’s bat (*Myotis formosus*), 26) Daubenton’s bat (*Myotis daubentonii*), 27) eastern long-eared bat (*Nyctophilus bifax*).

continued climate change (Flannigan et al. 2009), hibernators such as ground squirrels and bats may be able to ‘escape’ fire in underground hibernacula or in caves. However, arboreal hibernators such as marsupials, lemurs or dormice may be particularly vulnerable to fires occurring during hibernation. As a life history strategy, hibernation may have helped ancestral vertebrates survive catastrophic events and the world’s largest mass extinction ~252 million years ago (Whitney and Sidor 2020); whether hibernation allows extant vertebrates to survive catastrophic climate events remains to be seen.

Directions for future research. One challenge for studies of organismal responses to climate change is that responses to individual components of climate (e.g. warmer, drier) may be distinct, and sometimes in opposition. For example, earlier snowmelt in spring often begins a longer growing season, but also drier conditions. Our results show that longer growing seasons may often be positive for hibernators, but drier conditions are more reliably negative. Hence it remains useful for individual studies to separate these components and their resulting effects. Additionally, for most species it is still uncertain if chronic increases in warmer and drier conditions

are more of a challenge than acute climatic events such as extreme heat waves or precipitation events (Beever et al. 2017). Work that is able to include responses to both average and extreme climate variables will be extremely valuable (van de Pol et al. 2017).

Another challenge is that we know little about the relative magnitude of direct versus indirect effects of climate change on hibernator life histories. Reductions in snowpack can directly impact hibernators, by reducing thermal insulation of burrows and increasing the energetic cost of overwinter survival (Tafari et al. 2013). Reductions in snowpack and earlier snowmelt can also indirectly impact hibernators, reducing primary productivity in the short term, and plant abundance in the longterm; this can affect foraging of both herbivores (who rely on plant productivity) and insectivores (whose insect prey relies on plant productivity). Reductions in food availability in warmer or drier conditions may erode hibernator body condition, or reduce juvenile growth rates, with potentially severe consequences for overwinter survival and reproduction. Yet we found few studies that have reported hibernator growth and condition under different

climatic conditions (see Results above), much less quantified these indirect effects via changes to the resource base. This is an essential area of study.

Although this review focusses on how life history traits change in response to warmer and drier conditions, we have still much to learn in understanding how these traits co-vary and/or are traded against one another when resource allocation and investment decisions are made (i.e. life history trade-offs, Stearns 1992). Further, an understanding how these traits feed into fluctuating abundance, growth rates, transient and asymptotic dynamics is needed, along with forecasting models that would help predict future abundance, population growth or declines in light of future warming. As noted by Lane et al. (2018), the microevolution of phenotypic traits, phenological traits in particular, is presumed necessary to ensure long-term population viability; however it is incredibly difficult to distinguish between phenotypic plasticity and microevolutionary change when investigating phenological investment, which requires either genome-wide studies of selection or long-term detailed pedigrees and the funding to support such valuable, longitudinal individual-based studies worldwide.

Conclusion

This review highlights that phenological shifts constitute one of the most obvious consequences of climate change (Visser and Both 2005), yet, the timing of life history events (e.g. timing of migration, reproduction, hibernation) remains poorly understood in natura. Ecologists have been challenged in their ability to explain current phenological patterns, as well as predict how such patterns may change, and impact life history components, as our climate continues to warm. Eco-physiologists have recently made significant strides in elucidating the neuroendocrine mechanisms that govern seasonal and circannual rhythms (Chmura et al. 2019); population ecologists have been able to quantify the impact of phenological shifts on individual fitness and population dynamics (Ozgul et al. 2010, Cordes et al. 2020, Dobson et al. 2016) and evolutionary biologists are taking advantage of molecular tools that help document microevolutionary changes in phenological traits across generations (Lane et al. 2011, 2012, 2018, Boutin and Lane 2014). These recent advances have been made possible by the accumulation of long-term, individual-based data over multiple decades that we are only now beginning to exploit. It is our hope that further integration of insights from physiologists, evolutionary biologists and population ecologists working on wild populations will improve our collective understanding of the effects of seasonal climatic shifts on life history traits, namely growth, reproduction and survival, as key drivers of population persistence.

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Data availability statement

No new data were created or analyzed in this study. However, data gleaned from primary sources are available at <<https://doi.org/10.5061/dryad.z34tmpggs>>.

Supporting information

The Supporting information associated with this article is available with the online version.

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