Effects of climate change on life-history traits in hibernating mammals

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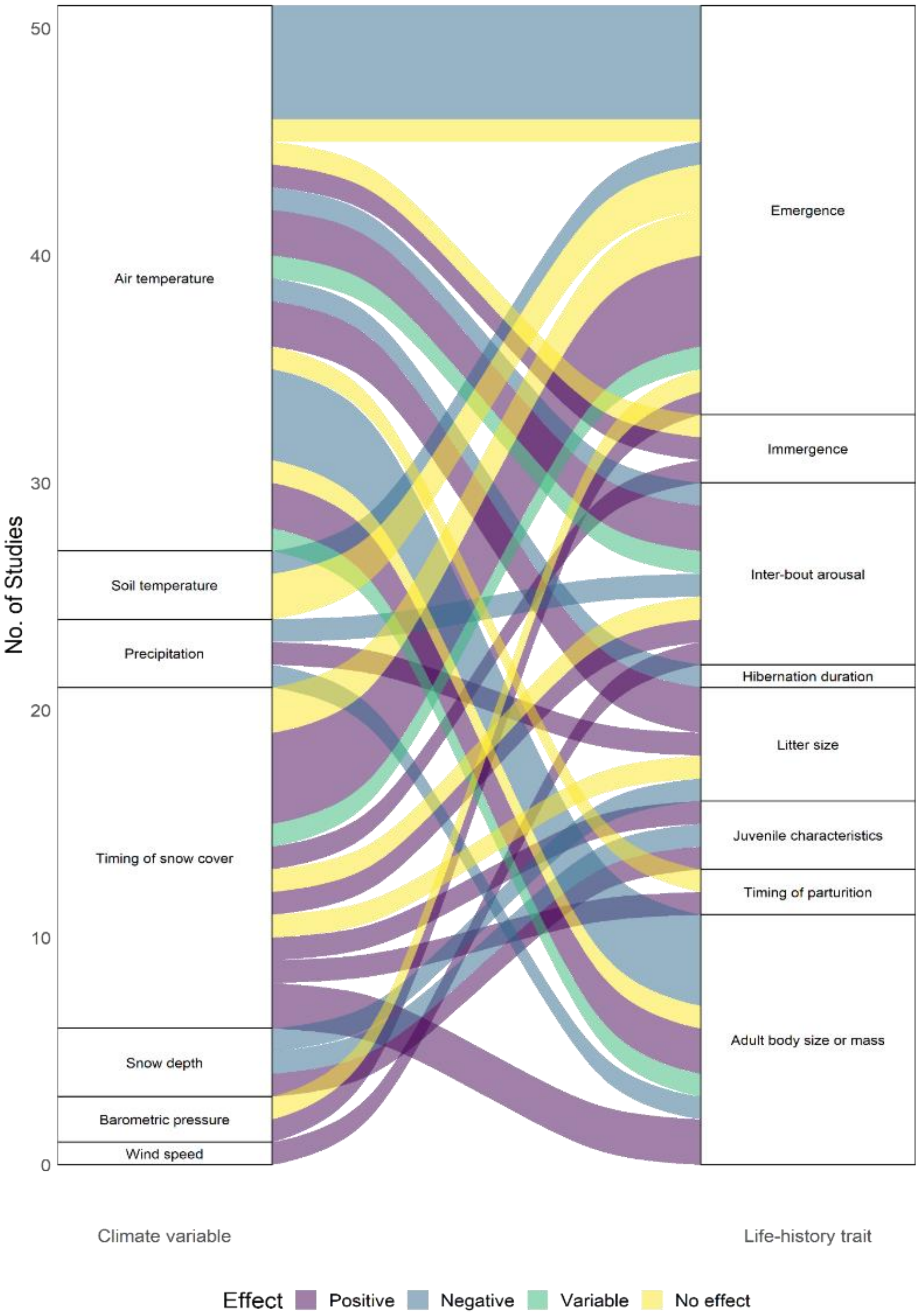
No. of Studies
50
40
30
20
10
0
Air temperature
Soil temperature
Precipitation
Timing of snow cover
Snow depth
Barometric pressure
Wind speed
Emergence
Immergence
Inter-bout arousal
Hibernation duration
Litter size
Juvenile characteristics
Timing of parturition
Adult body size or mass
Climate variable
Life-history trait
Effect
Positive
Negative
Variable
No effect

Graphical abstract

Climate change has the potential to influence life-history traits in mammals, with subsequent effects on fitness. Here, we reviewed studies examining the effects of changes in climatic variables on different life-history traits in hibernating mammals. The coloured lines indicate the directionality of associations, and line thickness indicates the number of studies that found each kind of association between a climatic variable and a life-history trait. We found that air temperature and the timing of snow cover are the climatic variables studied most frequently in association with life-history traits. The direction of associations often differed between species, although emergence date decreased (became earlier) with increasing air temperature in most studies and species. The timing of snow cover (i.e. start dates, end dates and duration of laying snow) was positively associated with a range of life-history traits in rodents. Hibernation emergence and adult body size/mass were the most commonly studied life-history traits, both of which may strongly affect reproductive success and survival. As hibernation behaviours are thought to have evolved as energy-saving mechanisms, environmental influences on changes in hibernation patterns, such as emergence and immergence, may subsequently influence other life-history traits. Such effects on energy allocation likely underlie some trait associations shown here. Future environmental changes may therefore affect individual fitness and population viability in hibernators.

Article type: Review

Title: Effects of climate change on life-history traits in hibernating mammals.

Running head: Effects of climate change on life-history in hibernators

Key words: hibernation, phenology, temperature, weather, environmental change

Word count: 9987

Abstract:

1. **Animals can respond to climate change through changes in behaviour, morphology or life-history traits. Changes in life-history traits do not occur independently, as they trade off or co-evolve with other traits.**
2. **Hibernation is a life-history trait used to cope with periods of low resource availability. The energetic and survival benefits of hibernation depend on environmental conditions. Climate change-induced changes in hibernation patterns are therefore likely to affect other life-history traits through trade-offs.**
3. **We systematically reviewed the literature to (i) identify studies testing for associations between climatic variables and life-history traits in hibernators, (ii) assess variation in responses between species, and (iii) determine whether changes in life-history traits associated with climate have subsequent effects on other life-history traits.**
4. **Air temperature was the most commonly measured climatic variable, and phenology of hibernation emergence was the most commonly studied life-history trait. Very few studies tested whether changes in life-history traits associated with climatic variables have subsequent effects on potentially co-adapted traits.**
5. **Despite being considered key life-history traits due to their potential to influence population dynamics, our search returned no studies on the effects**

of climatic variables on the age of primiparity or on the age distribution of reproduction.

6. **Directions of associations between climatic variables and life history traits often differed between species, and both species- and sex-specific variation occurred in response to climatic variables for some traits.**
7. **We highlight the importance of long-term, species-specific research, and the need for further studies on subsequent effects of climatic cues on coadapted traits to fully understand the potential for hibernators to respond to ongoing and future climate change.**

Introduction

Climate change is affecting species and ecosystems worldwide and contributing to global biodiversity loss (IPBES 2019). As long-term environmental change continues, understanding how climate change affects species characteristics will be increasingly important for wildlife conservation (Paniw et al. 2021).

Many species’ characteristics evolved to maximise fitness by influencing allocation of resources towards survival and reproduction; these characteristics are life-history traits (Endler 1986). Organisms’ life-history strategies are shaped by trade-offs in patterns of resource allocation between sets of co-adapted life-history traits (Box 1; Williams 1966, Stearns 1989). Trade-offs in resource allocation between reproduction and survival are a key mechanism of life-history evolution (Williams 1966). These trade-offs may occur at the genotypic or phenotypic level, or via mechanisms connecting the two (Stearns 1989). Phenotypic trade-offs concern traits that directly influence reproduction or survival and for which whole-organism measurements can be made (e.g. behavioural or morphological traits; Stearns 1989). Key traits measurable at the phenotypic level include litter size, offspring size, frequency of litter production, body size at maturity and the age distribution of reproductive effort (Stearns 1976).

Adjustment of life-history traits is a key route by which species may respond to environmental change (Root et al. 2003). Long-term changes in environmental cues, such as weather patterns, are associated with changes in phenological traits in a range of species (Walther et al. 2002), and may subsequently influence population demographics (Sæther et al. 2013). Environmental changes may also act indirectly, for instance by influencing resource availability at different times of year (Burgess et al. 2018). This may be particularly important for income breeders, where costs of reproduction are drawn from the immediately available resources (Jönsson 1997). However, changes in one trait in response to these cues may affect trade-offs with co-adapted traits, meaning that shifts in a single trait could potentially influence an organism's entire life-history.

Hibernation is a life-history trait found in approximately half of mammalian orders (Turbill et al. 2011). The term describes periods when organisms enter multi-day (>24h) bouts of torpor (Geiser & Ruf 1995). Physiological and metabolic characteristics of hibernation can vary broadly between species, leading to differences in the trade-offs experienced (Humphries et al. 2003, Nowack et al. 2019). There remains debate in the literature whether hibernation and daily torpor constitute a continuum of heterothermy (e.g. Boyles et al. 2013) or distinct physiological states (e.g. Ruf & Geiser 2015). This review focuses on mammals that show greatly depressed core body temperatures (often below 10°C) and metabolism for prolonged periods (on average more than a week, but up to several months). We refer to these as "prolonged hibernators" (Geiser & Ruf 1995).

The use of hibernation is associated with slow life-history strategies and can directly increase survival by reducing risks of predation or starvation when resources are limited (Turbill et al. 2011). Although hibernating species historically appear to have a lower extinction risk than non-hibernators, future effects of climate change on hibernators may depend on species' contexts (Geiser & Turbill 2009). Hibernation may also indirectly affect fitness via influences on other life-history traits. For instance, many species mate shortly after emerging from hibernation, thus the timing of hibernation emergence may influence the timing of parturition, with potential subsequent effects on fitness (Dobson & Michener 1995).

However, hibernation is also costly. Such costs may be ecological, such as increased vulnerability to predation (Estók et al. 2010), immunological, such as reduced immunocompetence (Prendergast et al. 2002), or physiological, such as telomere degradation at low temperatures (Nowack et al. 2019). Costs can be reduced through periodic returns to euthermy during hibernation, known as inter-bout arousals (IBAs;

reviewed by Humphries et al. 2003). However, IBAs are themselves energetically costly, depleting fat reserves and/or food resources, and can occur non-adaptively in response to disturbance (Speakman et al. 1991). This depletion may affect overwinter survival probability and resource availability for the early active season. Hence, IBAs may also directly and indirectly affect other life-history traits.

Prolonged hibernation is largely a seasonal trait. As such, aspects of its expression, such as the timing of emergence, can be influenced by climatic cues (Turbill & Prior 2016) in conjunction with internal mechanisms such as a circannual endogenous clock (Körtner & Geiser 2000). In seasonally active species, climatic factors are also likely to influence other life-history traits, either directly or indirectly. Hibernation behaviours are thought to have evolved as energy-saving mechanisms, often in response to adverse environmental conditions (Geiser 2013), therefore changing environmental conditions have the potential to strongly impact on energy allocation patterns in hibernators. Such changes in energy allocation may influence a range of other life-history traits, with subsequent impacts on individual fitness, and hence population viability (e.g. Lane et al. 2012, Maldonado-Chaparro et al. 2017). To predict how hibernators will react to future climatic changes, it is vital to understand the effects of climatic cues on life-history traits, individual fitness and population viability, and how these differ between species.

Here, we systematically review the literature to identify (a) studies testing for associations between climate and phenotypically-measurable life-history traits in hibernators, and which of these are most commonly studied, (b) whether the direction of these associations differs between species, and which species are most commonly studied and (c) the extent to which subsequent impacts of these effects on other life-history traits have been studied. We also discuss how climatic variables could influence life-history traits that have not been studied, and highlight the importance of integrative studies on multiple traits. These are necessary to fully understand the effects of climate change on taxa, and inform conservation planning.

Materials and methods

We used the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) framework (Liberati et al. 2009) to systematically search three databases (Web of Science, Scopus, Academic Ultimate) using terms related to key phenotypic life-history traits as described above and listed by Stearns (1989) and to climate change: hibernat* AND "climate change" OR climat* change OR global warming AND age at first reproduction OR "first reproduction" OR primiparity OR age distribution of reproduction OR reproductive effort OR litter size OR offspring quality OR social OR immergence OR "body size" OR emergence OR reproduction OR body mass OR "body mass" OR fitness OR age structure OR age structure of reproduction OR "reproductive effort" OR life-history. Searches were carried out on 23 September 2020. Abstracts were reviewed and articles excluded if they did not concern (i) extant mammal species, or (ii) prolonged hibernators (based on the criteria of Geiser & Ruf 1995; Figure 1). Review articles were also excluded.

Full manuscripts were accessed for the remaining articles, and details of species, response variables and explanatory variable(s) were extracted. Where single articles contained data on multiple species or life-history traits, each unique "species - response variable - explanatory variable" combination was considered separately, and hereafter referred to as a "study". In two articles, the responses of different species were analysed together, and we therefore treat them as a single study. Studies with the response variables "survival" or "fitness" were excluded as these variables were not considered to be specific phenotypically-measurable traits under our definition based on Stearns (1989; Box 1), but rather the outcome of trade-offs and stochastic processes.

Taxonomic and topical focus of hibernation research

Our literature search returned 313 unique articles. Due to the broad nature of our search, over half of the unique articles did not concern extant hibernating mammals, and many others mentioned climate change without testing for associations with climatic variables. Following screening (Figure 1), 57 studies from 26 articles were extracted (Table 1). Fifty-five studies examined relationships between climatic variables and life-history traits (Table 1; Appendix S1), whilst two studies focussed on subsequent effects on other life-history traits. Sixteen different climatic variables and 16 different response trait variables were measured.

To give a broader overview of responses, similar traits and climatic variables were grouped into categories with similar variables (Table 1; Appendix S1). Studies were also classified by taxonomic order. Among the 16 specific climatic variables, snowmelt date was the most commonly measured climatic variable, assessed in 23% of studies, followed by mean autumn air temperature (18%; Appendix S1). Mean annual air temperature, mean monthly soil temperature, total annual precipitation, start date of lying snow, duration of snow cover and hourly wind speed) were each studied only once (2%). When grouped into seven broad categories (air temperature, soil temperature, barometric pressure, precipitation, snow depth, timing of snow cover and wind speed), air temperature was the most commonly measured, occurring in 47% of studies (Appendix S1). Aspects of timing of snow cover, including snowmelt date and snow cover duration formed the second largest group (29%), and wind speed was the smallest group (2%).

The order Rodentia was the most commonly studied taxon (71%), followed by Chiroptera (25%), Eulipotyphla (2%) and Monotremata (2%; Figure 2). This is consistent with the proportion of hibernating species in each group (Constant et al. 2020; Fisher’s Exact Test, p = 0.03). Rodents were studied in relation to traits from all 9 trait classes in contrast to Chiroptera (three trait classes) and Eulipotyphla and Monotremata (one trait class each; Figure 2). Two of the 57 studies examined “secondary effects”, i.e., effect of a climatic variable on trait X, then the effect of trait X on trait Y. One of these examined the effects of body mass on the probability of successfully producing a litter, the other the effects of emergence date on timing of parturition.

Table 1. Studies on associations between climatic variables and life-history traits returned by the systematic literature review. Numbers in brackets represent the total number of studies for each group and sub-group.

Response trait category	Response trait	Climatic variable	Taxon	Species	Effect	Reference
Adult body size or mass (12)	Body condition (1)	Snowmelt date (1)	Rodentia	*Urocitellus parryii*	Positive	Sheriff et al. 2017
	Body mass (3)	Air temperature (winter) (1)	Rodentia	*Glis glis*	Variable	Fietz et al. 2020
		Precipitation (winter) (1)		*Cricetus cricetus*	Negative	Tissier et al. 2016
		Snowmelt date (1)		*Urocitellus parryii*	Positive	Sheriff et al. 2013
	Body size (2)	Air temperature (monthly) (1)	Rodentia	*Spermophilus xanthoprymnus*	Negative	Gür 2010
		Soil temperature (monthly) (1)		*Spermophilus xanthoprymnus*	Negative	
	Pre-hibernation body mass (6)	Air temperature (autumn) (6)	Chiroptera	*Barbastella barbastellus*	Positive	Ignaczak et al. 2019
				Myotis bechsteinii	Positive	
				Myotis daubentonii	No effect	
				Myotis myotis	Negative	
				Myotis nattereri	Negative	
				Plecotus auritus	Negative	
Hibernation emergence (18)	Emergence date (14)	Air temperature (autumn) (1)	Rodentia	*Zapus hudsonius*	Negative	Frey 2015
		Air temperature (spring) (1)	Chiroptera	*Myotis lucifugus*	No effect	Meyer et al. 2016
		Air temperature (spring) (4)	Rodentia	*Glis glis*	Negative	Adamík and Král 2008
				Glis glis	Negative	Fietz et al. 2020
				Marmota flaviventer	Negative	Edic et al. 2020
				Marmota flaviventer	Negative	Inouye et al. 2000
		Barometric pressure (spring) (2)	Chiroptera	*Myotis lucifugus*	Positive	Czenze & Willis 2015
				Myotis lucifugus	No effect	Meyer et al. 2016
		Snowmelt date (4)	Rodentia	*Marmota flaviventer*	Positive	Blumstein 2009

Hibernation emergence (cont.) (18)				*Marmota flaviventer*	Positive	Edic et al. 2020
				Urocitellus columbianus	Positive	Lane et al. 2012
				Urocitellus parryii	Positive	Sheriff et al. 2013
		Soil temperature (spring) (2)	Rodentia	*Urocitellus parryii*	Negative	
				Urocitellus parryii (males)	No effect	Sheriff et al. 2011
	Return to euthermy (4)	Snowmelt date (3)	Rodentia	*Urocitellus parryii*	No effect	Sheriff et al. 2013
				Urocitellus parryii (females)	Variable	Williams et al. 2017
				Urocitellus parryii (males)	No effect	
		Soil temperature (spring) (1)	Rodentia	*Urocitellus parryii*	No effect	Sheriff et al. 2013
Hibernation duration (1)	Hibernation duration (1)	Air temperature (annual) (1)	Rodentia	*16 rodent species*	Negative	Turbill & Prior 2016
Inter-bout arousal (8)	IBA frequency (8)	Air temperature (autumn) (1)	Monotremata	*Tachyglossus aculeatus setosus*	Negative	Nicol & Andersen 2002
		Air temperature (winter) (3)	Chiroptera	*9 bat species*	Positive	Barros et al. 2017
				Myotis lucifugus	Variable	Czenze et al. 2017
				Myotis nattereri	Positive	Hope & Jones 2013
		Precipitation (winter) (1)	Chiroptera	*9 bat species*	Negative	Barros et al. 2017
		Snowmelt date (2)	Rodentia	*Urocitellus parryii* (females)	Positive	Williams et al. 2017
				Urocitellus parryii (males)	No effect	
		Wind speed (1)	Chiroptera	*9 bat species*	Positive	Barros et al. 2017
Immergence (3)	Immergence date (3)	Air temperature (autumn) (2)	Eulipotyphla	*Erinaceus europaeus*	Positive	Rasmussen et al. 2019
			Rodentia	*Zapus hudsonius*	No effect	Frey 2015
		Timing of snow cover (1)	Rodentia	*Urocitellus parryii* (males)	Positive	Sheriff et al. 2011
Offspring growth (4)	Juvenile mass gain (2)	Proxy of environmental quality (1)	Rodentia	*Marmota flaviventer*	No effect	Paniw et al. 2020
				Marmota marmota	Positive	Canale et al. 2016

		Snow depth (1)	Rodentia	*Marmota marmota*	Negative	
	Juvenile structural growth (2)	Proxy of environmental quality (1)	Rodentia	*Marmota marmota*	Positive	
		Snow depth (1)	Rodentia	*Marmota marmota*	Positive	
Offspring recruitment (2)	Juvenile recruitment (2)	Proxy of environmental quality (1)	Rodentia	*Marmota flaviventer*	No effect	Paniw et al. 2020
		Snow start date (1)	Rodentia	*Urocitellus parryii*	Positive	Sheriff et al. 2017
Litter size (5)	Litter size (3)	Air temperature (spring) (1)	Rodentia	*Glis glis*	Positive	Fietz et al. 2020
		Snow depth (1)	Rodentia	*Marmota marmota*	Negative	Tafani et al. 2013
		Snowmelt date (1)	Rodentia	*Urocitellus parryii*	No effect	Sheriff et al. 2017
	Litter size (variation) (2)	Air temperature (monthly) (1)	Rodentia	*Marmota flaviventer*	Positive	Schwartz & Armitage 2005
		Precipitation (annual) (1)	Rodentia	*Marmota flaviventer*	Positive	
Timing of parturition (2)	Timing of parturition (2)	Air temperature (spring) (1)	Rodentia	*Glis glis*	No effect	Fietz et al. 2020
		Snowmelt date (1)	Rodentia	*Urocitellus parryii* (females)	Positive	Williams et al. 2017

Hibernation phenology

Hibernation has both fitness benefits and costs (Humphries et al. 2003), and the timing and expression of hibernation immergence and emergence, and IBA frequency, should therefore be optimised to maximise benefits and minimise costs (Boyles et al. 2020). Emergence traits were the most commonly studied broad trait category in our study (21% of studies), with emergence date being the most commonly studied specific life-history trait. For both taxa in which they were studied, Rodentia and Chiroptera (Figure 3), emergence dates became earlier in association with higher air temperatures in all but one study, where no effect was seen; however, in this study a positive association was found with snowmelt date (Lane et al. 2012). This suggests that the specific climatic variables most strongly associated with emergence timing may differ between species. For instance, yellow-bellied marmots *Marmota flaviventer* in Colorado emerged progressively earlier over the course of 20 years, in conjunction with increases in spring air temperatures. This was despite no change in average snowmelt date (Inouye et al. 2000). Conversely, female Columbian ground squirrels *Urocitellus columbianus* in Alberta progressively delayed emergence between 1992 and 2011 (Lane et al. 2012) as ordinal snowmelt dates also became later. There was a trend towards increasing spring temperatures during this period, but it was not statistically significant. Similar responses to delayed snowmelt (a one month delay in emergence after extreme weather) occurred in female arctic ground squirrels *Urocitellus parryii* (Williams et al. 2017). Female arctic ground squirrels had previously been shown to time emergence with rising soil temperatures (Williams et al. 2012), highlighting the importance of considering the use of multiple climatic variables.

Emergence dates may also be indirectly influenced by climate. Whilst associations between rising spring temperatures and earlier hibernation emergence were found in edible dormice *Glis glis* by Adamík & Král (2008), Fietz et al. (2020) observed that the strength of the relationship between emergence date and temperature strongly depended on food availability in the previous summer. Individuals of this fat-storing species with higher pre-emergence mass emerged later than lighter conspecifics, having lost a greater proportion of body mass (Fietz et al. 2020). This suggests that edible dormice use excess energy stores to remain in hibernation for longer. In little brown bats *Myotis lucifugus* and yellow-bellied marmots, by contrast, heavier individuals emerge from hibernation earlier (Czenze & Willis 2015, Edic et al. 2020), based on mid-winter and post-emergence masses respectively. These species reproduce earlier in the season than edible dormice, so that emerging with higher energy availability, in the form of greater body mass, may allow individuals to better withstand changing weather conditions or low food availability early in the season. Early emergence may also increase mating opportunities for species that mate following hibernation (Bernard 1985, Schwartz & Armitage 2005). In a food-storing hibernator, the European hamster *Cricetus cricetus*, experimentally supplementing food stores led to earlier hibernation emergence in both males and females, which also suggests that increased food availability may allow earlier emergence (Siutz et al. 2018). Nonetheless, this evidence suggests a mediating role of pre-hibernation food availability, which impacts on energy availability during and following hibernation. Pre-hibernation energy availability and food stores could also be influenced by weather conditions affecting resource availability or foraging ability prior to hibernation.

The differences in the direction of the relationships between body mass and emergence date might be related to the mating systems of the species concerned. Most seasonally-reproducing hibernators benefit from parturition early in the active season (Dobson & Michener 1995), which maximises time for offspring growth before hibernation, and early emergence allows earlier mating and/or parturition. This includes species that mate preceding or during hibernation (Sandell 1990). Heavier individuals may be better able to deal with climatic and resource uncertainty following early emergence, whilst lighter individuals are more likely to starve if emerging before sufficient resources are available. However, this is not the case in all species; for example, edible dormice reproduce late in the active season to synchronise with seed masting events, and may forego reproduction altogether in non-mast years (Ruf & Bieber 2020). Therefore, unlike many early-reproducing species, they do not gain a fitness advantage from early emergence.

Differences in mating systems and social structure between species may also influence emergence timing in other ways. The structure of hibernation groups may affect emergence timing in yellow-bellied marmots (Blumstein et al. 2004). Hibernation groups containing more adult males emerge earlier than those with fewer males, the number of males in a group representing a metric of reproductive competition (Blumstein 2009). In solitarily hibernating arctic ground squirrels, male hibernation emergence is related to dates of emergence of females, despite males appearing to use soil temperature as a cue for physiological exit from hibernation (i.e. return to euthermy; Sheriff et al. 2013). This pattern of male-before-female hibernation emergence is common among solitary hibernators due to sexual selection (Michener 1983). Whether this is influenced by sex-specific use of environmental cues is unknown for most species. However, in communally-hibernating little brown bats, although females emerge before males due to differences in the timing of reproductive investment (Willis 2017), both sexes appear to use falling barometric pressure as an emergence cue (Czenze & Willis 2015).

Far fewer studies (5%) in our search tested associations between climate and hibernation immergence compared to emergence (Table 1; Appendix S1), likely due to the difficulty of accurately recording immergence dates. The existing studies provide limited evidence that climatic factors directly influence immergence timing. Studies on juvenile arctic ground squirrels (Sheriff et al. 2015) and New Mexico jumping mice *Zapus hudsonius luteus* (Frey 2015) reported no association between climatic conditions and immergence dates. Conversely, juvenile European hedgehogs *Erinaceus europaeus* were recorded immerging later than previously recorded during an exceptionally mild autumn, which was attributed to later-than-usual food availability (Rasmussen et al. 2019). However, no relationship between body mass and hibernation immergence timing was found, and pre-hibernation masses of individuals in this study were above the suggested lower threshold of ~450 – 600 g for surviving hibernation (Bearman-Brown et al. 2020). However, effects of an endogenous circannual clock preventing immergence until a set time after birth for juveniles, as suggested by Sheriff et al. (2015), cannot be ruled out. Such circannual rhythms could delay immergence of late-born juveniles irrespective of body mass, but experimental research is required to disentangle these effects.

There is, however, suggestive evidence for indirect effects of climatic factors on immergence date, primarily via effects on body mass. Negative associations have been reported between ordinal immergence date and body mass prior to hibernation in edible dormice, irrespective of whether individuals reproduced that year (Bieber et al. 2014). It is also thought that water stress may play a role in triggering hibernation (Bintz 1984), although to our knowledge this has not been experimentally tested. For herbivores and granivores in particular, climatic effects on food and water availability could therefore indirectly affect immergence date via influences on body mass. Such indirect connections between immergence and climatic factors warrant further study.

Frequency of IBAs (periodic returns to euthermy) was the second most common subject of studies returned in our review. IBAs can be measured in the wild using implanted temperature dataloggers (e.g. Williams et al. 2011), temperature-sensitive collars (e.g. Dausmann et al. 2004) or thermal imaging cameras (Hayman et al. 2017). As non-fossorial hibernators, bats may be a more convenient subject for the study of IBAs. Indeed, bats accounted for 83% of IBA studies (Table 1). Studies of winter activity in ten bat species found increased activity levels (and, by extension, IBAs) at higher ambient temperatures (Hope & Jones 2013, Barros et al. 2017). This was particularly apparent as temperatures crossed thresholds for insect flight, providing feeding opportunities. Interestingly, negative associations between torpor bout duration and ambient temperature in adult little brown bats appear to be reversed in young-of-the-year, suggesting a condition- or age-dependent relationship (Czenze et al. 2017). Most studies on IBAs in bats returned by our search measured activity (i.e., flight) as a proxy for arousals. Nevertheless, IBAs are not always associated with physical activity (Trachsel et al. 1991, Hoelzl et al. 2016), and future research should consider such stationary IBAs, e.g. through the use of temperature telemetry (Czenze et al. 2017) or thermal imaging (Hayman et al. 2017), to fully understand the effects of winter weather on IBAs.

Reproduction

Several phenotypic traits can contribute to reproductive success, key among which are individual reproductive effort and reproductive timing. Individual reproductive effort has been defined as the proportion of resources invested into reproduction (Williams 1966), including production of sex cells, gestation and provision of nutrition (Trivers 1972). Measuring individual reproductive effort can therefore be complex, which is reflected in the range of response traits seen in our results. Of the 14 studies in this group, five different response variables were measured. These fell into three categories: “offspring growth”, including offspring growth rates and mass gain, “offspring recruitment” and “litter size”, including variation in and absolute litter size (Table 1). Litter size was the most commonly studied reproductive trait. In our results, reproductive traits were only studied in Rodentia.

Associations between climatic variables and litter size appear to be largely mediated by climatic effects on body mass. Successful parturition rates, offspring mass, litter size and juvenile winter survival rates all positively associate with maternal body mass in a range of hibernators (Dobson & Murie 1987, Tafani et al. 2013, Rubach et al. 2016). Long-term increases in litter size in yellow-bellied marmots (Maldonado-Chaparro et al. 2015) and declines in litter size in Alpine marmots *Marmota marmota* (Tafani et al. 2013) have both been attributed to the effects of warmer winters on body mass during hibernation. This demonstrates that effects can occur in opposing directions even in closely related species experiencing similar changes in weather patterns.

Studying multiple aspects of reproductive effort within individuals or populations will also help discern effects of climate change on reproductive success more clearly. For instance, within the same population and study period, Tafani et al. (2013) observed decreases in the litter sizes of Alpine marmots, while Canale et al. (2016) found no change in juvenile body mass. Although the findings of Tafani et al. (2013) may imply negative consequences for Alpine marmots, those of Canale et al. (2016) suggest that Alpine marmots may preferentially allocate resources to offspring quality over quantity. Maternal mass upon emergence also showed a declining trend during this period (although this was not significant; Tafani et al. 2013), suggesting that fewer resources were available for investment. Such preferential investment in offspring quality could aid overwinter survival by allowing juveniles to immerge at higher body masses. Declines in juvenile overwinter survival of Alpine marmots (Rézouki et al. 2016) are associated with more severe winters and decreases in marmot group sizes, as larger group sizes help to offset the energetic costs of hibernation for juveniles (Arnold 1990). Juveniles in better body condition may therefore have an increased chance of overwinter survival in smaller groups, as they have greater energy reserves than juveniles in poorer body condition. This suggests strong selection pressures on body condition (body size to mass ratio; Canale et al. 2016) of juvenile Alpine marmots for winter survival. Unfavourable weather conditions, such as high precipitation following hibernation emergence, is associated with unsuccessful breeding or offspring abandonment in some bat species (Ransome 1990, Grindal et al. 1992). As many bat species only produce a single offspring per breeding attempt, unsuccessful breeding or abandonment may incur a high fitness cost for individuals, particularly if climate change increases the incidence of such weather conditions.

In seasonal breeders, early breeding females generally have higher reproductive success (Dobson & Michener 1995). As parturition date is closely related to emergence date in many hibernating species (e.g. Lane et al. 2011), delayed emergence of adult females from hibernation may lead to reduced overwinter survival of their juveniles (Neuhaus 2000, Frick et al. 2010, Monclús et al. 2014) and lower fitness (Frick et al. 2010, Ozgul et al. 2010, Lane et al. 2012). Some species, particularly of Chiroptera, may also use daily torpor when pregnant, either due to inclement weather or low food availability. This may further delay parturition (Ransome 1990). Even in species that delay parturition until late in the active season, such as edible and hazel dormice, earlier-born juveniles often show increased survival during hibernation (Pilastro et al. 1994, Bieber et al. 2012).

Where relationships between parturition timing and hibernation emergence exist, costs of climate-induced delays in parturition can be offset by changes in reproductive investment. Both female Richardson’s *Urocitellus richardsonii* and Uinta ground squirrels *Urocitellus armatus* show differential allocation of maternal resources depending on the timing of parturition, with late reproducers producing fewer and larger offspring than early reproducers (Dobson & Michener 1995, Rieger 1996). Offspring survival during hibernation increases with body condition in many ground squirrel species (Murie & Boag 1984, Rieger 1996); therefore, investment in fewer, larger offspring late in the season maximises the winter survival probabilities of late-born offspring. Climate change may reduce the resource investment required to survive hibernation, for example through shorter or milder winters. Females may then be able to shift away from this tactic and towards larger litter sizes regardless of parturition timing. However, the number and size of neonates is physiologically limited unless adult size also increases.

There is also evidence of phenotypic differences in post-weaning growth rate and mass gain between early and late-born juveniles in garden dormice *Eliomys quercus* and European hedgehogs (Bunnell 2009, Stumpfel et al. 2017). Late-born juveniles grow faster than early born juveniles in both species. However, potential long-term fitness consequences of such early investment in rapid growth are unknown. In hazel dormice *Muscardinus avellanarius*, no long-term negative effects of late birth on lifetime reproductive success have been found among individuals who survived to reproductive age. However, late-born juveniles are less likely to survive to reproductive onset (Bieber et al. 2012).

Long-term changes in reproductive effort may manifest in many forms, as seen by the range of response variables measured in the studies found by our search (Table 1). Both inter- and intraspecific variation was found in the direction of responses, making it appear unlikely that assumptions can be made as to the response of other species without collecting species-specific observational data. In particular, species that generally produce only a single offspring per reproductive attempt, e.g., many hibernating bats, could be more strongly affected by climate-linked reductions in mean fitness than species producing larger litters. This may be particularly evident if climatic changes also negatively affect survival rates (e.g. Rézouki et al. 2016, Schorr & Siemers 2021), although the greater longevity and slower life-history of insectivorous bats compared to rodents might compensate for this. Additionally, our results suggest that the mechanisms linking climate to reproductive traits are not well studied. Changes in (for example) parturition timing or offspring size have the potential to strongly impact population dynamics, and so further studies in this area are warranted.

Body size and mass

The terms body size and mass are often used interchangeably, but may have different effects on life-history. Structural body size (e.g., length from snout to tail) initially increases over time in mammals and remains stable once structural growth is complete, whereas mass fluctuates within and between seasons. We found body mass to be measured much more frequently than body size (16% vs. 4% of total studies, Table 1) in relation to climate. Although body mass and body condition (mass to size ratio) are not themselves considered life-history traits, they can strongly influence a number of life-history traits and demographic processes (Ozgul et al. 2010, Paniw et al. 2020); these influences are discussed in previous sections.

Changes in body size as a response to climatic change have been suggested in a range of species (e.g. Teplitsky et al. 2009, Rode et al. 2010, Sheridan & Bickford 2011), but the magnitude and direction of observed changes differ across species (Gardner et al. 2011). Our search results returned three studies on body size, two of which examined body size in relation to spatial differences in air or soil temperature in Anatolian ground squirrels *Spermophilus xanthoprymnus* (Gür 2010), and one which examined longitudinal changes in juvenile body size in Alpine marmots (Canale et al. 2016). The need for experimental studies to disentangle the effects of climate on body size and mass was highlighted by Canale et al. (2016) who found negative associations between juvenile body size and date of vegetation onset, and juvenile body size and date of weaning. Date of vegetation onset and date of weaning may both be influenced by climatic factors. In spite of a sustained decline in body size over 22 years, no corresponding change in juvenile body mass was detected. If juvenile body size and mass were examined individually, different conclusions could be drawn; taken together, they suggest an increase in juvenile mass-to-size ratio during the study. This result could be interpreted as a positive effect on juvenile body condition. Conversely, smaller body sizes present a greater surface area-to-volume ratio, which may negatively affect energy retention during hibernation (Arnold 1990). It remains to be seen whether climate-associated declines in body size will affect long-term fitness.

Age distribution of reproductive effort

A key life-history trait of many hibernating species is delayed maturation, with offspring not reproducing until their second or third year. The age of primiparity can influence lifetime reproductive success (LRS) and mean fitness, potentially impacting population dynamics (Sæther et al. 2013). Some hibernators show intraspecific variation in age at primiparity (e.g. Dobson et al. 1999, Bieber et al. 2012), which often appears to be influenced by environmental conditions. Despite this, our search returned no studies on associations between climate and the age distribution of reproductive effort or age of primiparity in hibernators.

The most apparent route by which climate change may influence age at primiparity is through indirect effects on body mass, for instance through changing resource availability. The probability of yearling breeding in Columbian ground squirrels, European hamsters, and Daubenton's and Natterer's bats appears to be positively related to resource availability (Dobson & Murie 1987, Tissier et al. 2016, Linton & Macdonald 2020). For all of these species, climate could affect both the quality and quantity of food available in the future (Rosenblatt & Schmitz 2016). Differential effects of climate on adult and juvenile overwinter survival, as seen in Uinta ground squirrels, could also indirectly allow more yearling breeding. Warmer winters reduce adult survival but not juvenile survival, giving yearlings a better chance of occupying a high-quality, resource rich territory (Falvo et al. 2019). Such potential indirect effects of climate on the age distribution of reproduction warrant further research.

To predict effects of climate change on age at primiparity, a greater understanding of the underlying causes and consequences of variation in the majority of hibernators is required. Current research suggests that body mass, as discussed above, is likely to be a major influence on the age of primiparity. Therefore, in species where climatic conditions are leading to changes in body mass (e.g., Ozgul et al. 2010, Tissier et al. 2016), it is likely that contributions of younger age classes to population growth will also change. Understanding the relative importance of these contributions is therefore important to accurately project effects of climate on long-term population dynamics.

Social factors

Many hibernators display a degree of sociality. For instance, among twelve marmot species where social organisation has been classified, only woodchucks *Marmota monax* are "solitary" (Armitage 2007). Increased complexity in social organisation and structure is positively correlated with large body size, late primiparity and short vegetation growing seasons (Armitage 1981). These traits are also often associated with harsher climates and lower resource availability (e.g. Bronson 1979, Dobson & Murie 1987). Hence, aspects of social structure, such as group size and cohesion (Kappeler 2019), could be influenced by climate change. Despite this, our results found no studies examining the effects of climate change on social structure.

Social hibernation of extended family groups occurs in some marmot species (Armitage 2007). Evidence for some benefits of social thermoregulation during hibernation, particularly for juveniles, has been found in Alpine and hoary marmots *Marmota caligata* (Arnold 1990, Patil et al. 2013). In general, larger group sizes have been associated with lower overwinter mass loss and improved overwinter survival in juveniles. However, in hoary marmots, the positive correlation between group size and juvenile overwinter survival is weaker than the negative correlation between juvenile overwinter survival and the pacific decadal oscillation index, an indicator of winter severity (Patil et al. 2013). Additionally, the benefits of social hibernation may be affected by climate-induced changes in other traits, as discussed above. For instance, long-term declines in litter size of Alpine marmots lead to fewer subordinates in socially hibernating groups, which negatively affects juvenile overwinter survival. This further reduces subordinate numbers in the following year, forming a negative feedback loop (Arnold 1990, Rezouki et al. 2016). These studies suggest that the benefits of social thermoregulation may not outweigh the costs of winter conditions under future climate scenarios, but further research is needed in this area.

Sex-specific life-history variation, including in hibernation patterns, occurs in several hibernating species (e.g. Sheriff et al. 2013, Norquay & Willis 2014). Where differences are influenced by environmental conditions, climate change could drive sex-specific phenological mismatches. For instance, in male arctic ground squirrels, a pre-emergence return to euthermy is associated with soil temperature in concert with an endogenous circannual clock (Sheriff et al. 2013), whilst physical emergence in males is related to female emergence timing (Williams et al. 2017). However, female emergence is associated with snowmelt date (Williams et al. 2017). Although these climatic factors are often correlated, associations with different cues could lead to asynchronous change between male and female emergence dates. In turn, this could lead to increased reproductive competition, or delayed parturition if males are not fully reproductively competent when females emerge. As this pattern of male-before-female emergence is common among hibernating species (Michener 1983), understanding variation in cue use is important for anticipating changes in reproductive competition and patterns.

Effects of climate change on social organisation, and potential mediating effects of social organisation on other life-history traits, are understudied. However, they may be crucial for predicting how population dynamics respond to changing environmental conditions. In particular, due to the greater ease of determining maternity than paternity, many studies focus solely on female life-histories. This provides an incomplete understanding. For instance, although female Columbian ground squirrels are emerging from hibernation progressively later in association with delays in winter snowmelt (Lane et al. 2012), whether males are experiencing a similar delay has not been studied. If, as in arctic ground squirrels, male emergence is associated with a different cue, emergence timing of the sexes could become mis-matched.

Conclusions and future directions

Associations between many climatic variables, most commonly air temperature, and life-history traits have been demonstrated in hibernators (Table 1). Several different climatic variables are linked to hibernation emergence dates. Emergence dates have subsequent impacts on fitness-related traits such as litter size, timing of parturition and offspring survival rates. Several studies also demonstrated direct connections between climatic variables and these fitness-related traits (Table 1, Appendix S1). However, in spite of several multi-decadal studies on hibernators (Hayes et al. 2017), many questions on how climatic factors influence hibernation, and interactions between climate, hibernation and other life-history traits, still remain. Although associations such as those described above have been found, the specific mechanisms underlying these associations, and their potential subsequent effects, are less well studied. A focus on whole-lifecycle questions is needed to fully understand the flexibility of responses of hibernators to ongoing and future climatic changes, and the potential subsequent life-history and population demographic effects. Additionally, indirect effects of climate on hibernators mediated by, for instance, food availability, need to be considered more closely.

Rodents were the most commonly studied taxon in our review (Figure 2). This may reflect rodents' generally short generation time and ease of manipulation in the field, and the prior existence of many long-term studies on rodents (Hayes et al. 2017). However, the diversity of responses to climatic factors seen among even ecologically similar and closely related species (e.g. Culina et al. 2017) suggests that results from rodents should not be applied to other taxa without further research. Nevertheless, despite the differences in life-history strategies between rodents and insectivorous bats, the two largest and most common taxa in our results, many potential effects of future climate change appear to be largely similar. For instance, timing of parturition affects reproductive success across species in both taxa, and parturition timing may be strongly influenced by climate. However, the population-level impacts on these taxa from such changes are likely to be different due to their different life-history strategies. Additionally, some traits have been much more heavily studied in some taxa than others (e.g., IBAs in bats), making generalisations across taxa difficult.

Most long-term studies of hibernators occur at high elevations, such as the Alps and Rocky Mountains. Although climate change may be leading to, for example, decreases in snow depth in these areas, snow is still more-or-less guaranteed at these high elevations. Much less research has been conducted on prolonged hibernators in more variable climates, where average winter temperatures often do not fall below zero, and snow does not fall every year. The benefits of hibernation other than saving energy, such as predation avoidance (Bieber et al. 2014), also warrant further research. Examining the causes and flexibility of differences in hibernation patterns within wide-ranging species may aid in understanding the potential for hibernation patterns to buffer species against changing climatic conditions.

In our systematic review, only two articles examined the effects of climate-induced changes in one trait on subsequent traits. This may be due to publishing patterns, where such studies are published separately. Although many studies have investigated trade-offs between life-history traits in hibernators, as discussed here, evidence suggests that these trade-offs may be altered under changing environmental conditions (e.g. McLean et al. 2016). Climate change is an urgent and topical issue, but fully understanding its impacts requires integrative research on its indirect and long-term effects on life-history and population dynamics.

Box 1. Key terms used in this review.

Glossary.

Life-history trait – an aspect of behaviour, physiology or anatomy that influences an organism's energy allocation to reproduction and/or fitness (Endler, 1986).

Life-history strategy – a genetically-based set of decision rules that control the expression of traits

Prolonged hibernator – animal that demonstrates multi-day (>24 hours) periods of torpor and associated large depressions in body temperature and metabolism.

Emergence – an individual's physical exit from a hibernaculum (e.g., burrow or cave) following a final return to euthermy

Immergence – an individual's entry into hibernation

Inter-bout arousal (IBA) – periodic, short-term returns to euthermy that are experienced by hibernators between multi-day bouts of torpor

Table 1. Studies on associations between climate and life-history traits returned by the systematic literature review. Numbers in brackets represent total numbers of studies for each category and sub-category.

Figure 1. Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) diagram showing the process of study identification and selection. Literature searching was carried out using the Web of Science, Scopus and Academic Ultimate databases. Articles were excluded if they did not concern (i) extant mammals (ii) prolonged hibernators [Box 1] (iii) phenotypically measured life-history traits [Box 1], and/or (iv) climatic variables, based on the abstract or the full text. From each article, unique species-response variable- explanatory variable combinations were extracted and treated as separate studies.

Figure 2. Number of studies of each life-history trait group in each taxon returned by the systematic search. The overall proportion of studies found in each taxon was consistent with the number of known hibernating species in each taxonomic group (Fisher's Exact Test, p = 0.03).

Appendix S1. Associations between climatic variables and life-history traits in hibernators returned by a systematic review. Line thickness is proportional to the number of studies on a particular climatic variable and life-history trait combination, and lines are labelled with the number of papers found for each variable. Monthly and annual values represent the mean value of the variable for this time period. "Proxy of environmental quality" represents a latent variable used to capture a number of climatic and environmental variables by Paniw et al. (2020).

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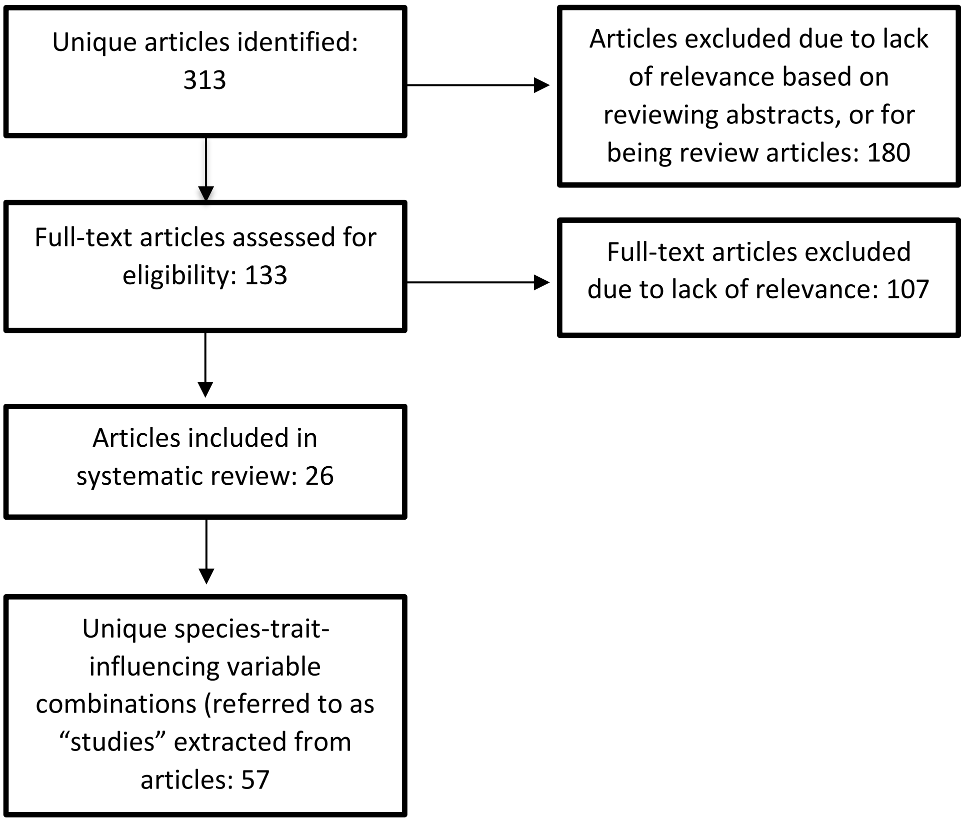
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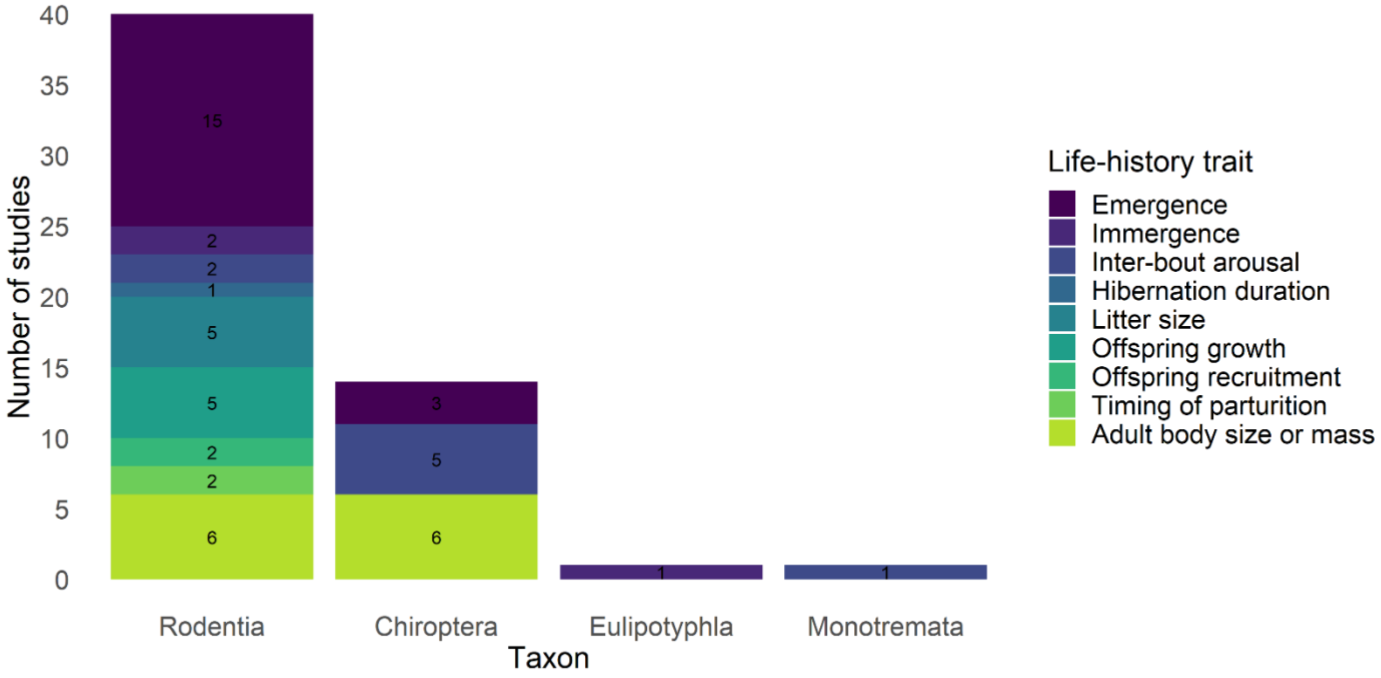
Unique species-trait-influencing variable combinations (referred to as "studies" extracted from articles: 57

Figure 1.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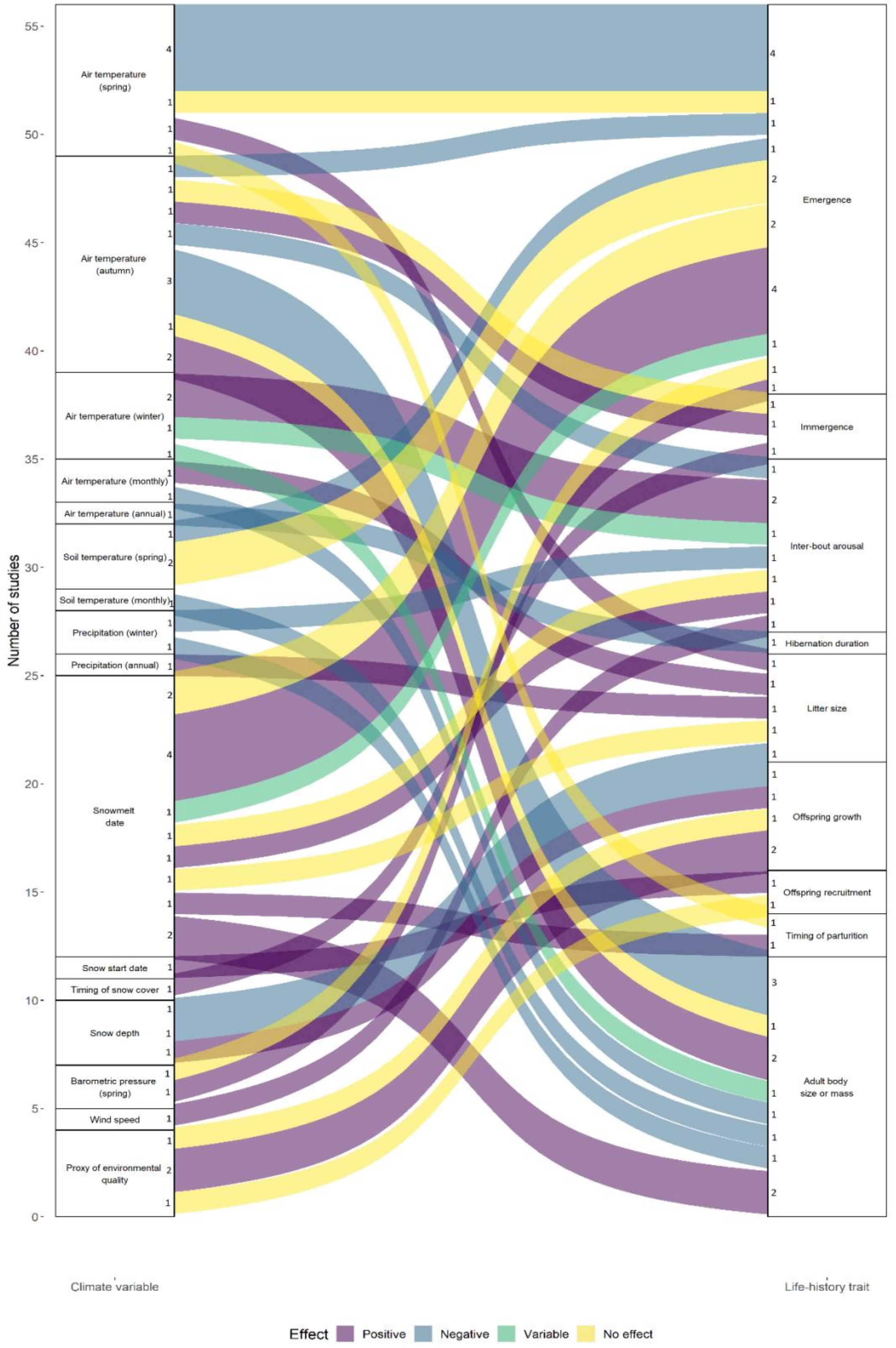
6
1
1
Rodentia
Chiroptera
Eulipotyphla
Monotremata
Taxon
Life-history trait
Emergence
Immergence
Inter-bout arousal
Hibernation duration
Litter size
Offspring growth
Offspring recruitment
Timing of parturition
Adult body size or mass

Figure 2.

Supplementary Online Materials



Appendix S1. Associations between climatic variables and life-history traits in hibernators returned by a systematic review. Line thickness is proportional to the number of studies on a particular climatic variable and life-history trait combination, and lines are labelled with the number of papers found for each variable. Monthly and annual values represent the mean value of the variable for this time period. “Proxy of environmental quality” represents a latent variable used to capture a number of climatic and environmental variables by Paniw et al. (2020).