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

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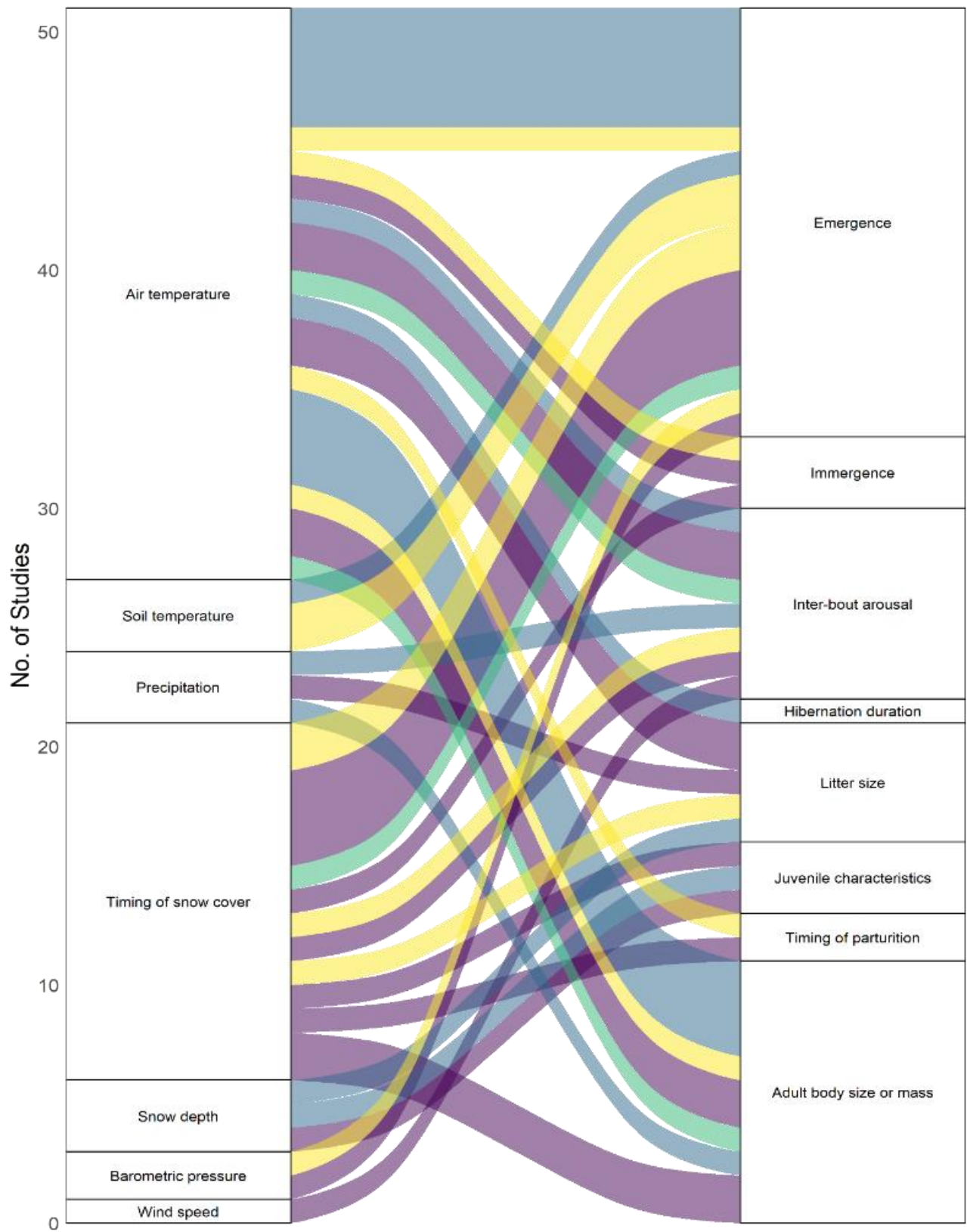
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Climate variable

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.

1 **Article type: Review**

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

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

4 **Key words: hibernation, phenology, temperature, weather, environmental**  
5 **change**

6 **Word count: 9987**

7 **Abstract:**

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

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

29 6. Directions of associations between climatic variables and life history traits  
30 often differed between species, and both species- and sex-specific variation  
31 occurred in response to climatic variables for some traits.

32 7. We highlight the importance of long-term, species-specific research, and the  
33 need for further studies on subsequent effects of climatic cues on coadapted  
34 traits to fully understand the potential for hibernators to respond to ongoing  
35 and future climate change.

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## 55 **Introduction**

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

60

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

73

74 Adjustment of life-history traits is a key route by which species may respond to  
75 environmental change (Root et al. 2003). Long-term changes in environmental cues, such as  
76 weather patterns, are associated with changes in phenological traits in a range of species  
77 (Walther et al. 2002), and may subsequently influence population demographics (Sæther et  
78 al. 2013). Environmental changes may also act indirectly, for instance by influencing  
79 resource availability at different times of year (Burgess et al. 2018). This may be particularly  
80 important for income breeders, where costs of reproduction are drawn from the immediately  
81 available resources (Jönsson 1997). However, changes in one trait in response to these

82 cues may affect trade-offs with co-adapted traits, meaning that shifts in a single trait could  
83 potentially influence an organism's entire life-history.

84

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

95

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

104

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



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

115

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

129

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

138

## 139 **Materials and methods**

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

152

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

162

## 163 **Taxonomic and topical focus of hibernation research**

164 Our literature search returned 313 unique articles. Due to the broad nature of our search,  
165 over half of the unique articles did not concern extant hibernating mammals, and many

166 others mentioned climate change without testing for associations with climatic variables.  
167 Following screening (Figure 1), 57 studies from 26 articles were extracted (Table 1). Fifty-  
168 five studies examined relationships between climatic variables and life-history traits (Table 1;  
169 Appendix S1), whilst two studies focussed on subsequent effects on other life-history traits.  
170 Sixteen different climatic variables and 16 different response trait variables were measured.

171

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

184

185 The order Rodentia was the most commonly studied taxon (71%), followed by Chiroptera  
186 (25%), Eulipotyphla (2%) and Monotremata (2%; Figure 2). This is consistent with the  
187 proportion of hibernating species in each group (Constant et al. 2020; Fisher's Exact Test,  $p$   
188 = 0.03). Rodents were studied in relation to traits from all 9 trait classes in contrast to  
189 Chiroptera (three trait classes) and Eulipotyphla and Monotremata (one trait class each;  
190 Figure 2). Two of the 57 studies examined "secondary effects", i.e., effect of a climatic  
191 variable on trait X, then the effect of trait X on trait Y. One of these examined the effects of  
192 body mass on the probability of successfully producing a litter, the other the effects of  
193 emergence date on timing of parturition.

194

195

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

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

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

199 **Hibernation phenology**

200 Hibernation has both fitness benefits and costs (Humphries et al. 2003), and the timing and  
201 expression of hibernation immergence and emergence, and IBA frequency, should therefore  
202 be optimised to maximise benefits and minimise costs (Boyles et al. 2020). Emergence traits  
203 were the most commonly studied broad trait category in our study (21% of studies), with  
204 emergence date being the most commonly studied specific life-history trait. For both taxa in  
205 which they were studied, Rodentia and Chiroptera (Figure 3), emergence dates became  
206 earlier in association with higher air temperatures in all but one study, where no effect was  
207 seen; however, in this study a positive association was found with snowmelt date (Lane et al.  
208 2012). This suggests that the specific climatic variables most strongly associated with  
209 emergence timing may differ between species. For instance, yellow-bellied marmots  
210 *Marmota flaviventer* in Colorado emerged progressively earlier over the course of 20 years,  
211 in conjunction with increases in spring air temperatures. This was despite no change in  
212 average snowmelt date (Inouye et al. 2000). Conversely, female Columbian ground squirrels  
213 *Urocitellus columbianus* in Alberta progressively delayed emergence between 1992 and  
214 2011 (Lane et al. 2012) as ordinal snowmelt dates also became later. There was a trend  
215 towards increasing spring temperatures during this period, but it was not statistically  
216 significant. Similar responses to delayed snowmelt (a one month delay in emergence after  
217 extreme weather) occurred in female arctic ground squirrels *Urocitellus parryii* (Williams et  
218 al. 2017). Female arctic ground squirrels had previously been shown to time emergence with  
219 rising soil temperatures (Williams et al. 2012), highlighting the importance of considering the  
220 use of multiple climatic variables.

221

222 Emergence dates may also be indirectly influenced by climate. Whilst associations between  
223 rising spring temperatures and earlier hibernation emergence were found in edible dormice  
224 *Glis glis* by Adamík & Král (2008), Fietz et al. (2020) observed that the strength of the  
225 relationship between emergence date and temperature strongly depended on food  
226 availability in the previous summer. Individuals of this fat-storing species with higher pre-



227 emergence mass emerged later than lighter conspecifics, having lost a greater proportion of  
228 body mass (Fietz et al. 2020). This suggests that edible dormice use excess energy stores  
229 to remain in hibernation for longer. In little brown bats *Myotis lucifugus* and yellow-bellied  
230 marmots, by contrast, heavier individuals emerge from hibernation earlier (Czenze & Willis  
231 2015, Edic et al. 2020), based on mid-winter and post-emergence masses respectively.  
232 These species reproduce earlier in the season than edible dormice, so that emerging with  
233 higher energy availability, in the form of greater body mass, may allow individuals to better  
234 withstand changing weather conditions or low food availability early in the season. Early  
235 emergence may also increase mating opportunities for species that mate following  
236 hibernation (Bernard 1985, Schwartz & Armitage 2005). In a food-storing hibernator, the  
237 European hamster *Cricetus cricetus*, experimentally supplementing food stores led to earlier  
238 hibernation emergence in both males and females, which also suggests that increased food  
239 availability may allow earlier emergence (Siutz et al. 2018). Nonetheless, this evidence  
240 suggests a mediating role of pre-hibernation food availability, which impacts on energy  
241 availability during and following hibernation. Pre-hibernation energy availability and food  
242 stores could also be influenced by weather conditions affecting resource availability or  
243 foraging ability prior to hibernation.

244

245 The differences in the direction of the relationships between body mass and emergence date  
246 might be related to the mating systems of the species concerned. Most seasonally-  
247 reproducing hibernators benefit from parturition early in the active season (Dobson &  
248 Michener 1995), which maximises time for offspring growth before hibernation, and early  
249 emergence allows earlier mating and/or parturition. This includes species that mate  
250 preceding or during hibernation (Sandell 1990). Heavier individuals may be better able to  
251 deal with climatic and resource uncertainty following early emergence, whilst lighter  
252 individuals are more likely to starve if emerging before sufficient resources are available.  
253 However, this is not the case in all species; for example, edible dormice reproduce late in the  
254 active season to synchronise with seed masting events, and may forego reproduction

255 altogether in non-mast years (Ruf & Bieber 2020). Therefore, unlike many early-reproducing  
256 species, they do not gain a fitness advantage from early emergence.

257

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

272

273 Far fewer studies (5%) in our search tested associations between climate and hibernation  
274 immergence compared to emergence (Table 1; Appendix S1), likely due to the difficulty of  
275 accurately recording immergence dates. The existing studies provide limited evidence that  
276 climatic factors directly influence immergence timing. Studies on juvenile arctic ground  
277 squirrels (Sheriff et al. 2015) and New Mexico jumping mice *Zapus hudsonius luteus* (Frey  
278 2015) reported no association between climatic conditions and immergence dates.

279 Conversely, juvenile European hedgehogs *Erinaceus europaeus* were recorded immerging  
280 later than previously recorded during an exceptionally mild autumn, which was attributed to  
281 later-than-usual food availability (Rasmussen et al. 2019). However, no relationship between  
282 body mass and hibernation immergence timing was found, and pre-hibernation masses of

283 individuals in this study were above the suggested lower threshold of ~450 – 600 g for  
284 surviving hibernation (Bearman-Brown et al. 2020). However, effects of an endogenous  
285 circannual clock preventing immergence until a set time after birth for juveniles, as  
286 suggested by Sheriff et al. (2015), cannot be ruled out. Such circannual rhythms could delay  
287 immergence of late-born juveniles irrespective of body mass, but experimental research is  
288 required to disentangle these effects.

289

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

299

300 Frequency of IBAs (periodic returns to euthermia) was the second most common subject of  
301 studies returned in our review. IBAs can be measured in the wild using implanted  
302 temperature dataloggers (e.g. Williams et al. 2011), temperature-sensitive collars (e.g.  
303 Dausmann et al. 2004) or thermal imaging cameras (Hayman et al. 2017). As non-fossorial  
304 hibernators, bats may be a more convenient subject for the study of IBAs. Indeed, bats  
305 accounted for 83% of IBA studies (Table 1). Studies of winter activity in ten bat species  
306 found increased activity levels (and, by extension, IBAs) at higher ambient temperatures  
307 (Hope & Jones 2013, Barros et al. 2017). This was particularly apparent as temperatures  
308 crossed thresholds for insect flight, providing feeding opportunities. Interestingly, negative  
309 associations between torpor bout duration and ambient temperature in adult little brown bats  
310 appear to be reversed in young-of-the-year, suggesting a condition- or age-dependent

311 relationship (Czenze et al. 2017). Most studies on IBAs in bats returned by our search  
312 measured activity (i.e., flight) as a proxy for arousals. Nevertheless, IBAs are not always  
313 associated with physical activity (Trachsel et al. 1991, Hoelzl et al. 2016), and future  
314 research should consider such stationary IBAs, e.g. through the use of temperature  
315 telemetry (Czenze et al. 2017) or thermal imaging (Hayman et al. 2017), to fully understand  
316 the effects of winter weather on IBAs.

317

### 318 **Reproduction**

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

329

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

339

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

363

364 In seasonal breeders, early breeding females generally have higher reproductive success  
365 (Dobson & Michener 1995). As parturition date is closely related to emergence date in many  
366 hibernating species (e.g. Lane et al. 2011), delayed emergence of adult females from

367 hibernation may lead to reduced overwinter survival of their juveniles (Neuhaus 2000, Frick  
368 et al. 2010, Monclús et al. 2014) and lower fitness (Frick et al. 2010, Ozgul et al. 2010, Lane  
369 et al. 2012). Some species, particularly of Chiroptera, may also use daily torpor when  
370 pregnant, either due to inclement weather or low food availability. This may further delay  
371 parturition (Ransome 1990). Even in species that delay parturition until late in the active  
372 season, such as edible and hazel dormice, earlier-born juveniles often show increased  
373 survival during hibernation (Pilastro et al. 1994, Bieber et al. 2012).

374

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

388

389 There is also evidence of phenotypic differences in post-weaning growth rate and mass gain  
390 between early and late-born juveniles in garden dormice *Eliomys quercus* and European  
391 hedgehogs (Bunnell 2009, Stumpf et al. 2017). Late-born juveniles grow faster than early  
392 born juveniles in both species. However, potential long-term fitness consequences of such  
393 early investment in rapid growth are unknown. In hazel dormice *Muscardinus avellanarius*,  
394 no long-term negative effects of late birth on lifetime reproductive success have been found

395 among individuals who survived to reproductive age. However, late-born juveniles are less  
396 likely to survive to reproductive onset (Bieber et al. 2012).

397

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

411

## 412 **Body size and mass**

413 The terms body size and mass are often used interchangeably, but may have different  
414 effects on life-history. Structural body size (e.g., length from snout to tail) initially increases  
415 over time in mammals and remains stable once structural growth is complete, whereas mass  
416 fluctuates within and between seasons. We found body mass to be measured much more  
417 frequently than body size (16% vs. 4% of total studies, Table 1) in relation to climate.

418 Although body mass and body condition (mass to size ratio) are not themselves considered  
419 life-history traits, they can strongly influence a number of life-history traits and demographic  
420 processes (Ozgul et al. 2010, Paniw et al. 2020); these influences are discussed in previous  
421 sections.

422

423 Changes in body size as a response to climatic change have been suggested in a range of  
424 species (e.g. Teplitsky et al. 2009, Rode et al. 2010, Sheridan & Bickford 2011), but the  
425 magnitude and direction of observed changes differ across species (Gardner et al. 2011).  
426 Our search results returned three studies on body size, two of which examined body size in  
427 relation to spatial differences in air or soil temperature in Anatolian ground squirrels  
428 *Spermophilus xanthoprymnus* (Gür 2010), and one which examined longitudinal changes in  
429 juvenile body size in Alpine marmots (Canale et al. 2016). The need for experimental studies  
430 to disentangle the effects of climate on body size and mass was highlighted by Canale et al.  
431 (2016) who found negative associations between juvenile body size and date of vegetation  
432 onset, and juvenile body size and date of weaning. Date of vegetation onset and date of  
433 weaning may both be influenced by climatic factors. In spite of a sustained decline in body  
434 size over 22 years, no corresponding change in juvenile body mass was detected. If juvenile  
435 body size and mass were examined individually, different conclusions could be drawn; taken  
436 together, they suggest an increase in juvenile mass-to-size ratio during the study. This result  
437 could be interpreted as a positive effect on juvenile body condition. Conversely, smaller body  
438 sizes present a greater surface area-to-volume ratio, which may negatively affect energy  
439 retention during hibernation (Arnold 1990). It remains to be seen whether climate-associated  
440 declines in body size will affect long-term fitness.

441

#### 442 **Age distribution of reproductive effort**

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



451

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

464

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

473

#### 474 **Social factors**

475 Many hibernators display a degree of sociality. For instance, among twelve marmot species  
476 where social organisation has been classified, only woodchucks *Marmota monax* are  
477 "solitary" (Armitage 2007). Increased complexity in social organisation and structure is  
478 positively correlated with large body size, late primiparity and short vegetation growing

479 seasons (Armitage 1981). These traits are also often associated with harsher climates and  
480 lower resource availability (e.g. Bronson 1979, Dobson & Murie 1987). Hence, aspects of  
481 social structure, such as group size and cohesion (Kappeler 2019), could be influenced by  
482 climate change. Despite this, our results found no studies examining the effects of climate  
483 change on social structure.

484

485 Social hibernation of extended family groups occurs in some marmot species (Armitage  
486 2007). Evidence for some benefits of social thermoregulation during hibernation, particularly  
487 for juveniles, has been found in Alpine and hoary marmots *Marmota caligata* (Arnold 1990,  
488 Patil et al. 2013). In general, larger group sizes have been associated with lower overwinter  
489 mass loss and improved overwinter survival in juveniles. However, in hoary marmots, the  
490 positive correlation between group size and juvenile overwinter survival is weaker than the  
491 negative correlation between juvenile overwinter survival and the pacific decadal oscillation  
492 index, an indicator of winter severity (Patil et al. 2013). Additionally, the benefits of social  
493 hibernation may be affected by climate-induced changes in other traits, as discussed above.  
494 For instance, long-term declines in litter size of Alpine marmots lead to fewer subordinates in  
495 socially hibernating groups, which negatively affects juvenile overwinter survival. This further  
496 reduces subordinate numbers in the following year, forming a negative feedback loop  
497 (Arnold 1990, Rezouki et al. 2016). These studies suggest that the benefits of social  
498 thermoregulation may not outweigh the costs of winter conditions under future climate  
499 scenarios, but further research is needed in this area.

500

501 Sex-specific life-history variation, including in hibernation patterns, occurs in several  
502 hibernating species (e.g. Sheriff et al. 2013, Norquay & Willis 2014). Where differences are  
503 influenced by environmental conditions, climate change could drive sex-specific phenological  
504 mismatches. For instance, in male arctic ground squirrels, a pre-emergence return to  
505 euthermia is associated with soil temperature in concert with an endogenous circannual clock  
506 (Sheriff et al. 2013), whilst physical emergence in males is related to female emergence

507 timing (Williams et al. 2017). However, female emergence is associated with snowmelt date  
508 (Williams et al. 2017). Although these climatic factors are often correlated, associations with  
509 different cues could lead to asynchronous change between male and female emergence  
510 dates. In turn, this could lead to increased reproductive competition, or delayed parturition if  
511 males are not fully reproductively competent when females emerge. As this pattern of male-  
512 before-female emergence is common among hibernating species (Michener 1983),  
513 understanding variation in cue use is important for anticipating changes in reproductive  
514 competition and patterns.

515

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

526

## 527 **Conclusions and future directions**

528 Associations between many climatic variables, most commonly air temperature, and life-  
529 history traits have been demonstrated in hibernators (Table 1). Several different climatic  
530 variables are linked to hibernation emergence dates. Emergence dates have subsequent  
531 impacts on fitness-related traits such as litter size, timing of parturition and offspring survival  
532 rates. Several studies also demonstrated direct connections between climatic variables and  
533 these fitness-related traits (Table 1, Appendix S1). However, in spite of several multi-decadal  
534 studies on hibernators (Hayes et al. 2017), many questions on how climatic factors influence

535 hibernation, and interactions between climate, hibernation and other life-history traits, still  
536 remain. Although associations such as those described above have been found, the specific  
537 mechanisms underlying these associations, and their potential subsequent effects, are less  
538 well studied. A focus on whole-lifecycle questions is needed to fully understand the flexibility  
539 of responses of hibernators to ongoing and future climatic changes, and the potential  
540 subsequent life-history and population demographic effects. Additionally, indirect effects of  
541 climate on hibernators mediated by, for instance, food availability, need to be considered  
542 more closely.

543

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

557

558 Most long-term studies of hibernators occur at high elevations, such as the Alps and Rocky  
559 Mountains. Although climate change may be leading to, for example, decreases in snow  
560 depth in these areas, snow is still more-or-less guaranteed at these high elevations. Much  
561 less research has been conducted on prolonged hibernators in more variable climates,  
562 where average winter temperatures often do not fall below zero, and snow does not fall

563 every year. The benefits of hibernation other than saving energy, such as predation  
564 avoidance (Bieber et al. 2014), also warrant further research. Examining the causes and  
565 flexibility of differences in hibernation patterns within wide-ranging species may aid in  
566 understanding the potential for hibernation patterns to buffer species against changing  
567 climatic conditions.

568

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

576

577 **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 euthermia

Immergence – an individual's entry into hibernation

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

578

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

582

583 **Figure 1. Preferred Reporting Items for Systematic Reviews and Meta-Analyses**  
584 **(PRISMA) diagram showing the process of study identification and selection.**

585 **Literature searching was carried out using the Web of Science, Scopus and Academic**  
586 **Ultimate databases. Articles were excluded if they did not concern (i) extant mammals**  
587 **(ii) prolonged hibernators [Box 1] (iii) phenotypically measured life-history traits [Box**  
588 **1], and/or (iv) climatic variables, based on the abstract or the full text. From each**  
589 **article, unique species-response variable- explanatory variable combinations were**  
590 **extracted and treated as separate studies.**

591

592

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

597

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

605

606

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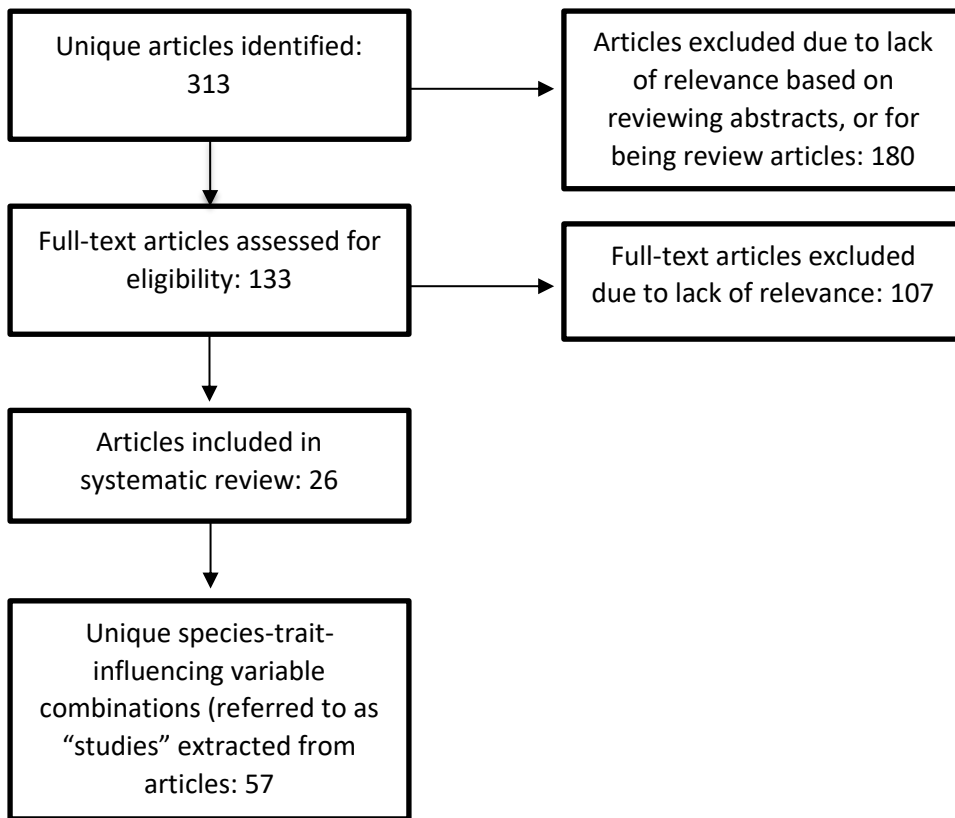


Figure 1.

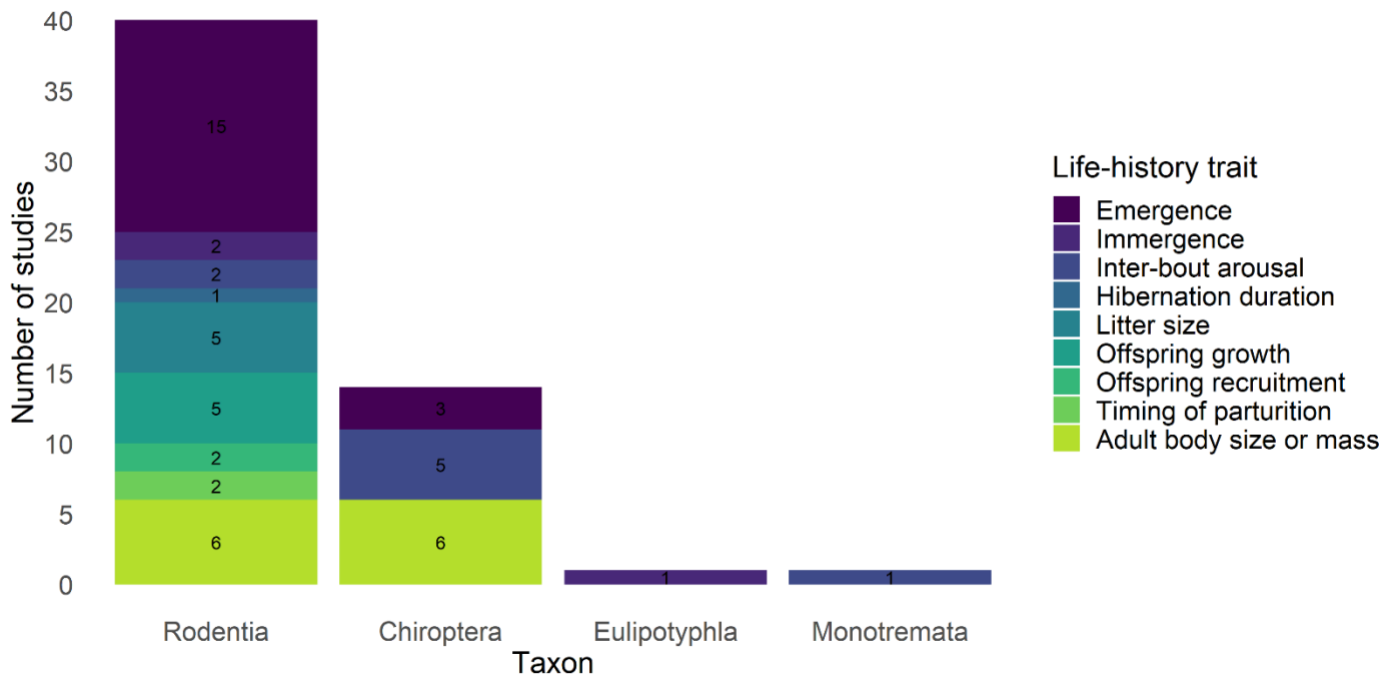
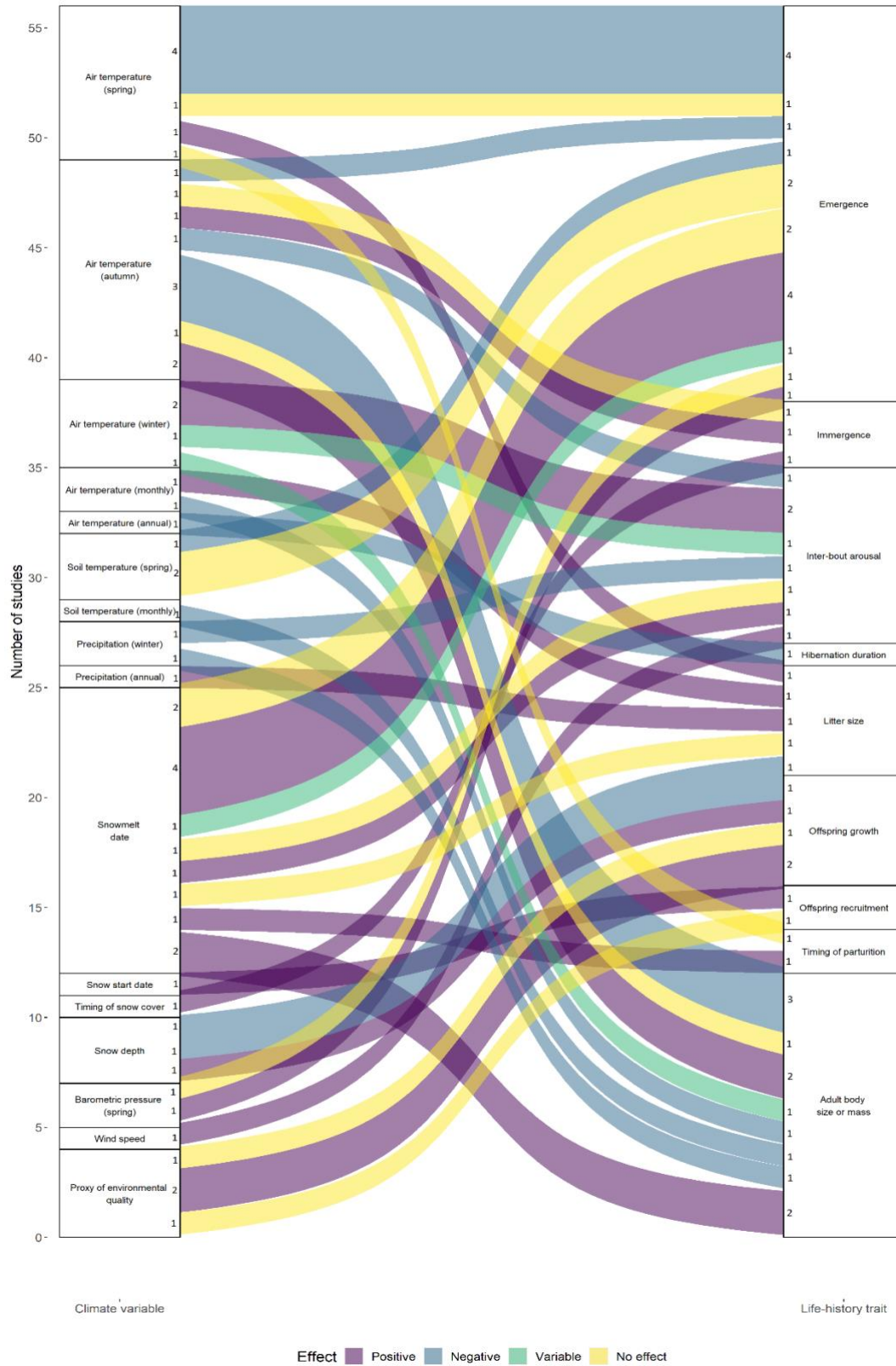


Figure 2.

# 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).**