



HAL
open science

Integrating mortality risks and the adaptiveness of hibernation

Théo Constant, Sylvain Giroud, Vincent Viblanc, Mathilde Tissier, Patrick Bergeron, F Stephen Dobson, Caroline Hahold

► **To cite this version:**

Théo Constant, Sylvain Giroud, Vincent Viblanc, Mathilde Tissier, Patrick Bergeron, et al.. Integrating mortality risks and the adaptiveness of hibernation. *Frontiers in Physiology*, 2020. hal-02732950

HAL Id: hal-02732950

<https://hal.science/hal-02732950>

Submitted on 2 Jun 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Integrating mortality risks and the adaptiveness of hibernation

Théo Constant¹, Sylvain Giroud², Vincent Viblanc¹, Mathilde L. Tissier³, Patrick Bergeron³, F. Stephen Dobson⁴, Caroline Habol^{1*}

¹UMR7178 Institut pluridisciplinaire Hubert Curien (IPHC), France, ²University of Veterinary Medicine Vienna, Austria, ³Bishop's University, Canada, ⁴Auburn University, United States

Submitted to Journal:
Frontiers in Physiology

Specialty Section:
Environmental, Aviation and Space Physiology

Article type:
Review Article

Manuscript ID:
512953

Received on:
18 Nov 2019

Revised on:
21 May 2020

Frontiers website link:
www.frontiersin.org

In review

Conflict of interest statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest

Author contribution statement

T.C.: conception and drafting S.G., V.V., M.L.T., P.B., S.F.D., C.H.: substantial contributions to the conception and revision

Keywords

Life History, activity pattern, time and energy allocation, Trade off, hibernator, temporal organization of activity, predation, Size

Abstract

Word count: 255

Low mortality rate is often associated with slow life history, and so far, has mainly been assessed through examinations of specific adaptations and lifestyles that limit mortality risk. However, the organization of activity time budgets also needs to be considered, since some activities and the time afforded for performing them may expose animals to higher mortality risks such as increased predation and/or increased metabolic stress, including oxidative stress. We examined the extent of activity time budgets contribution to explaining variation in life history traits in mammals. We specifically focused on hibernating species because of their marked seasonal cycle of activity/inactivity associated with very different mortality risks. Hibernation is considered a seasonal adaptation to prolonged periods of food shortage and cold. This inactivity period may also reduce both extrinsic and intrinsic mortality risks, by decreasing exposure to predators and drastically reducing metabolic rate. In turn, reduction in mortality may explain why hibernators have slower life history traits than non-hibernators of the same size. Using phylogenetically controlled models, we tested the hypothesis that longevity was positively correlated with the hibernation season duration (the time spent between emergence and emergence from the hibernaculum or den) across 82 different mammal species. We found that longevity increased significantly with hibernation season duration, an effect that was particularly strong in small hibernators (< 1.5kg) especially for bats. These results confirm that hibernation not only allows mammals to survive periods of energy scarcity, but further suggest that activity time budgets may be selected to reduce mortality risks according to life history pace.

Contribution to the field

Hibernation is widely considered as an adaptation to a seasonal decrease in food resources and ambient temperatures. If the remarkable physiological aspects of hibernation have been widely studied, fewer studies have focused on its ecological and evolutionary significance. In this study, we investigate whether hibernation, in addition to its survival benefits to face energy stress, may have evolved to limit other risk of mortality. The article is composed of a phylogenetic meta-analysis showing the patterns of association between hibernation season duration and longevity across mammalian hibernators. Our main conclusion is that hibernation season duration has a positive effect on longevity, and this effect is significantly greater small hibernators (<1.5kg) especially for bats, which are assumed to have a higher risk of predation and energy constraints, than larger species. Therefore, our article provides new evidence that hibernation duration may have evolved to limit mortality risk in some species.

Integrating mortality risk and the adaptiveness of hibernation

1 Théo Constant¹, Sylvain Giroud², Vincent A. Viblanc¹, Mathilde L. Tissier³, Patrick Bergeron³, F.
2 Stephen Dobson^{1,4}, Caroline Habold^{1*}

3 ¹Université de Strasbourg, CNRS, IPHC, UMR 7178, Strasbourg, France

4 ²Research Institute of Wildlife Ecology, Department of Interdisciplinary Life Sciences, University of
5 Veterinary Medicine, Vienna, Austria

6 ³Department of Biological Sciences, Bishop's University, 2600 College St., Sherbrooke, Quebec,
7 Canada, J1M 1Z7

8 ⁴Department of Biological Sciences, Auburn University, Auburn, AL 36849, USA

9 *Correspondence to Caroline Habold: caroline.habold@iphc.cnrs.fr

10

11

12

13

14

15

16

17

18

19 **Abstract**

20 Low mortality rate is often associated with slow life history, and so far, has mainly been assessed
21 through examinations of specific adaptations and lifestyles that limit mortality risk. However, the
22 organization of activity time budgets also needs to be considered, since some activities and the time
23 afforded for performing them may expose animals to higher mortality risks such as increased predation
24 and/or increased metabolic stress, including oxidative stress. We examined the extent of activity time
25 budgets contribution to explaining variation in life history traits in mammals. We specifically focused
26 on hibernating species because of their marked seasonal cycle of activity/inactivity associated with
27 very different mortality risks. Hibernation is considered a seasonal adaptation to prolonged periods of
28 food shortage and cold. This inactivity period may also reduce both extrinsic and intrinsic mortality
29 risks, by decreasing exposure to predators and drastically reducing metabolic rate. In turn, reduction in
30 mortality may explain why hibernators have slower life history traits than non-hibernators of the same
31 size. Using phylogenetically controlled models, we tested the hypothesis that longevity was positively
32 correlated with the hibernation season duration (the time spent between immergence and emergence
33 from the hibernaculum or den) across 82 different mammal species. We found that longevity increased
34 significantly with hibernation season duration, an effect that was particularly strong in small
35 hibernators (< 1.5kg) especially for bats. These results confirm that hibernation not only allows
36 mammals to survive periods of energy scarcity, but further suggest that activity time budgets may be
37 selected to reduce mortality risks according to life history pace.

38 **Keywords:** *activity patterns, hibernation, life history, temporal organization of activity, time and*
39 *energy allocations, trade-off, longevity, mortality risk.*

40 1 **Introduction**

41

42 Energy is the fundamental requirement for life. Its acquisition, storage, and metabolic use shape
43 the diversity of lifestyles in all living organisms (Brown et al., 2004). Because energy availability to
44 organisms is limited under natural conditions, in terms of its acquisition in time and space, as well as
45 its quantity and quality, organisms have to simultaneously maximize investments into all biological
46 functions, and to compromise the allocation of metabolic energy among competing demands
47 (Hirshfield and Tinkle, 1975; Lack, 1966; Reznick, 1985; Williams, 1966). For example, demographic
48 characteristics may affect energy investments among biological traits such as growth, reproduction,
49 and somatic maintenance. These trade-offs have led to the evolution of specific life history strategies
50 (Stearns, 1992).

51 Attributes of life histories generally scale with body size such that large animal species usually
52 take longer to develop and mature, have lower annual reproductive rates, and live longer compared to
53 small species (Blueweiss et al., 1978; Speakman, 2005). However, life history variations that are
54 specific to a particular body size are also observed along a fast-slow continuum (Bielby et al., 2007;
55 Dobson and Oli, 2007; Jeschke and Kokko, 2009; Jones et al., 2008; Oli, 2004). For a given body size,
56 most species trade off investments between reproduction and self-maintenance. For example, a species
57 with fast life history strategy will exhibit faster growth, earlier reproduction, larger annual reproductive
58 investment, and reduced maximum life span compared to a species with a slow life history strategy,
59 which will typically promote self-maintenance and survival over reproduction (but see Bielby et al.,
60 2007; Jeschke and Kokko, 2009).

61 The evolution of the fast-slow continuum in life history strategies appears to be contingent upon
62 individual mortality risk (Healy et al., 2019; Martin, 2015; Promislow and Harvey, 1990). Individual
63 mortality can be due to either intrinsic (wear-and-tear of the body) or extrinsic factors, such as

Time dimension of allocation trade-offs in hibernators

64 predation, disease, or environmental hazards. Species with slow life histories typically exhibit
65 adaptations that limit both sources of mortality (Lewis et al., 2013; MacRae et al., 2015; Munshi-South
66 and Wilkinson, 2010; Wu and Storey, 2016; Blanco and Sherman, 2005; Healy, 2015; Healy et al.,
67 2014; Holmes and Austad, 1994; Shattuck and Williams, 2010; Sibly and Brown, 2007; Turbill et al.,
68 2011; Wilkinson and South, 2002). Besides these molecular (such as oxidative stress tolerance),
69 physiological/anatomical (such as chemical protection, horns and antlers) or lifestyle (such as
70 arboreality) adaptations that reduce mortality risk, the organization of activity time budgets should be
71 particularly important in shaping the variety of life histories observed in the wild. Mortality rates may
72 change depending on the time allocated to each activity, resulting in trade-offs for which both time and
73 energy can be optimized. For instance, activities that contribute the most to reproductive success are
74 often energy-intensive (Alonso-Alvarez et al., 2004) and associated with higher risks of extrinsic
75 mortality (Magnhagen, 1991). However, the temporal dimension of energy allocation trade-offs in
76 relation to the evolution of life history strategies has been little examined (see Healy et al., 2014).

77 Here, we first examined the extent to which patterns of relative activity and inactivity can
78 explain variation in life history traits in mammals. We specifically focused on hibernating species
79 because of their marked seasonal cycle of activity/inactivity, which is associated with very different
80 risks of mortality. From an intrinsic perspective, hibernation is a period of metabolic depression where
81 energy requirements are reduced to minimal levels compared to the active season (Ruf and Geiser,
82 2015). It has been suggested that energy restriction slows down the aging process (Walford and
83 Spindler, 1997; Masoro, 2006) and is associated with an enhancement of somatic maintenance
84 (Shanley and Kirkwood, 2000). From an extrinsic perspective, even if mortality during hibernation
85 occurs, hibernating mammals are usually hidden in burrows or shelters, which may reduce risks of
86 predation, infections or injuries for several continuous months. As a result, hibernating species
87 generally exhibit lower rates of mortality than similar-sized non-hibernating species during part of the

Time dimension of allocation trade-offs in hibernators

88 year, resulting in slower life history strategies (Turbill et al., 2011; Wilkinson and South, 2002).
89 However, previous studies linking hibernation to longevity considered hibernation as a binary trait (if
90 animals hibernate or not), rather than a continuous adaptive response (hibernation season duration) that
91 allows animals to restrict their period of activity during parts of the year. Yet, early data from captivity
92 highlight a positive correlation between longevity and hibernation duration in Turkish hamsters
93 (*Mesocricetus brandti*) (Lyman et al., 1981). In addition, a strong negative effect of mean annual
94 temperature on hibernation season duration and annual survival rate, which is highly correlated with
95 longevity (Turbill et al, 2011), has been shown among populations of hibernating rodent species
96 (Turbill and Prior, 2016) This raises the question of whether, across hibernating mammals the time
97 spent being inactive (hibernation season duration) influences maximal longevity, a key feature
98 characteristic of fast and slow life history strategies

99 In the present study, we tested for a positive association between the hibernation season duration
100 and longevity across 82 mammalian species. For this examination, we tested for effect of body size on
101 longevity while controlling statistically for phylogeny. If indeed hibernation season duration is part of
102 a strategy allowing minimizing mortality, we predicted that longer hibernation season duration should
103 be positively associated with species maximum longevity, especially in small mammals (< 1.5 kg) that
104 exhibit greater longevity than non-hibernators of the same size (Turbill et al. 2011). In addition, if
105 metabolic reduction during hibernation slows aging (Lyman et al., 1981; Turbill et al., 2013; Wu and
106 Storey, 2016), we predicted that the effect of hibernation season duration on longevity should increase
107 with the percentage of metabolic reduction during hibernation compared to euthermia.

108 2 Material and methods

109 2.1 Review criteria

110

Time dimension of allocation trade-offs in hibernators

111 We conducted the review using the search engine Google Scholar (<https://scholar.google.com>)
112 and considered articles up to and including December 2019. We based our survey on the hibernating
113 species listed in Ruf and Geiser (2015) and Turbill et al (2011), and further identified nine other species,
114 mainly ground squirrels and bats, not mentioned in any of the lists. All the 152 hibernators that were
115 examined in this process are summarized in Electronic Supplementary Materials (see Table S1). We
116 excluded species for which hibernation was restricted to only a few populations or under specific
117 conditions, namely two species, the black-tailed prairie dogs (*Cynomys ludovicianus*; Gummer, 2005;
118 Lehmer et al., 2006) and the polar bears (*Ursus maritimus*; Amstrup and DeMaster, 2003). We did not
119 include non-seasonal hibernating species capable of entering multi-day torpor at any time of the year.
120 Indeed, for such cases, it is difficult to accurately measure the time spent in hibernation over a year,
121 which may also vary considerably among individuals and between years. Thus, we excluded
122 hibernating elephant shrew species (*Elephantulus* sp.) and hibernating marsupials with the exception
123 of the mountain pygmy possum (*Burramys parvus*), reported to be a seasonal hibernator (Geiser and
124 Körtner, 2010; Lovegrove et al., 2001).

125

126 2.2 Longevity and body mass data

127

128 Data on maximum longevity, hereafter referred as longevity, and average body mass for the list
129 of hibernating species previously identified were mainly obtained from the AnAge data base (The
130 Animal Aging and Longevity Database; https://genomics.senescence.info/species/search_list.php;
131 Human Ageing and Genomic Resources; Magalhães and Costa, 2009), and complemented these data
132 with information from the PanTHERIA data base (<https://ecologicaldata.org/wiki/pantheria>;
133 Ecological Archives, Ecological Society of America; Jones et al., 2009) from two reviews on
134 mammalian longevity (Heppell et al., 2000; Wilkinson and South, 2002) or from a specific search in

Time dimension of allocation trade-offs in hibernators

135 Google Scholar combining the following terms: “longevity” OR “life history” AND scientific or
136 common names of species. For this specific search in Google Scholar, we considered both old and new
137 nomenclatures for ground squirrel species, and only selected long-term field studies since they provide
138 a good estimate of maximum longevity. Moreover, we specifically investigated the source of the data
139 (captive vs. wild) and only retained longevity data where the source was available, to control for
140 captivity effects on longevity (see Electronic Supplementary Material, Table S2 for references).

141 We determined the arboreality lifestyle of the species in order to statistically control (see below
142 section 2.5) for higher longevity (Healy et al., 2014; Kamilar et al., 2010; Shattuck and Williams,
143 2010). We conducted a review of peer-reviewed scientific journal Mammalian Species
144 (<https://academic.oup.com/mspecies>) and used Google Scholar. The search criteria were based on
145 combining the following terms: "arboreal" OR "semi-arboreal" OR "climb tree" AND scientific or
146 common names of species. We completed our search by examining the mammalian lifestyle databases
147 of the following articles (Healy et al., 2014; Hidasi-Neto et al., 2015). Our arboreality factor includes
148 16 arboreal and semi-arboreal species, which feed, nest, or escape from predators, at least frequently,
149 by climbing into trees (see Electronic Supplementary Materials, Table S2).

150

151 **2.3 Hibernation season duration data**

152 **2.3.1 Reviewing strategy**

153

154 Relatively few studies have investigated hibernation duration with body temperature recorders
155 on wild mammals. However, several studies have estimated hibernation season duration from capture-
156 mark-recapture records or direct observations, thus assessing periods of inactivity. Although for some
157 species, the duration of hibernation measured as the period between the first and last torpor bout is

Time dimension of allocation trade-offs in hibernators

158 probably shorter than the period of inactivity (Siutz et al., 2016; Williams et al., 2014; Young, 1990) ,
159 these measures should still provide reasonable estimates of the duration of energy savings, thereby
160 allowing species to be compared with each other.

161 We reviewed the literature to retrieve estimates of the hibernation season duration as the time
162 (in days) spent between immergence and emergence from the hibernaculum or den (with little or no
163 movement outside). The search criteria were based on combining the following terms: “hibernation”
164 OR “hibernation duration” OR “denning” (exclusively for bears) OR “roosting” (exclusively for bats)
165 AND scientific or common names of species. In order to minimize heterogeneity in the scales at which
166 the data were measured (e.g. individual, population), we considered maximum hibernation season
167 duration obtained from same-sex adult groups, either male or female depending on the species (and
168 recorded maximum hibernation season duration from overall population data when more precise data
169 were unavailable).

171 2.3.2 Inclusion and exclusion criteria

172
173 We prioritized studies for which the methodology for estimating hibernation season duration of
174 is described (capture-mark-recapture, direct observation and body temperature recording). These
175 criteria included 64 species. We also included studies based on road kills as an index of
176 activity/inactivity. This criterion has already been used to evaluate changes in hedgehog abundance
177 (Bright et al., 2015; Morris and Morris, 1988; Wembridge et al., 2016) and was used for 2 species in
178 our data set (Algerian hedgehog (*Atelerix algirus*) and Southern white-breasted hedgehog (*Erinaceus*
179 *concolor*)). Finally, in cases where the above criteria were not available, we included studies for which

Time dimension of allocation trade-offs in hibernators

180 a precise hibernation period was mentioned but the methodology could not be assessed. This criterion
181 included 16 species (see Electronic Supplementary Material; Table S2, labeled species)

182 We excluded studies for which periods of extreme inactivity were measured only once in a
183 population. This criterion excluded three maximum hibernation season data: 8 months for the little
184 pocket mouse (*Perognathus longimembris*; Kenagy and Bartholomew, 1985); 6 months for the long-
185 tailed pocket mouse (*Chaetodipus formosus*; Kenagy and Bartholomew, 1985); and 11 months for the
186 Eastern chipmunk (*Tamias striatus*; Munro et al., 2008).

187 The availability or absence of data (longevity and hibernation season duration) in the literature
188 for the 152 species examined is specified in Electronic Supplementary Materials (see Table S1). In
189 total, our literature search allowed inclusion of 82 hibernating mammal in the analyses including 80
190 placental mammals, 27 bats, one marsupial (the mountain pygmy possum) and one monotreme (the
191 short-beaked echidna (*Tachyglossus aculeatus*)). Longevity, body mass and hibernation season
192 duration data for these species are available in Electronic Supplementary Materials (see Table S2).

193

194 **2.4 Phylogenetic data**

195

196 We downloaded 100 phylogenetic mammalian trees from <http://vertlife.org/phylosubsets/> (see
197 Upham et al., 2019), focusing on the 82 species in our data set (see Electronic Supplementary Material,
198 Table S2). These trees were used to construct strict consensus trees for the hibernating species of our
199 study, where the included clades were those present in all the 100 phylogenetic mammalian trees
200 (Paradis, 2011). Because we ran subsequent analyses on different subsets of the data (see section 2.5
201 below), we constructed separate phylogenetic trees on (1) the full hibernator data set (N = 82 species),
202 (2) the data set excluding bats (N = 55 species), (3) the data set with only deep hibernator (see below)

Time dimension of allocation trade-offs in hibernators

203 excluding bats (N = 46 species) and (4) the data set excluding bats and hibernators > 1.5 kg (N = 44
204 species) (see Electronic Supplementary Material, Fig S1).

205 The rationale for eliminating bats from some analyses was to compare the specific effect of
206 hibernation season duration on longevity between bats which have very distinct characteristics (i.e.,
207 flight capacity, highly gregarious behavior during hibernation (Austad and Fischer, 1991)) and other
208 hibernators.

209 The metabolic rate during torpor is not known for all hibernating species studied (Ruf and
210 Geiser, 2015). To test the prediction that the effect of hibernation season duration on longevity should
211 increase with metabolic reduction, we compared the effect of hibernation season duration on the
212 longevity of two groups including (all hibernators excluding bats) or excluding (only deep hibernators
213 without bats) species reducing their energy expenditure during hibernation by less than 90% compared
214 to the euthermic state. These comprise *Ursidae* species and the European badger (*Meles meles*) that
215 reduce their total energy expenditure from 33 to 75% during hibernation compared to the euthermic
216 state (Hellgren, 1998; Ruf and Geiser, 2015; Tøien et al., 2011; Watts and Jonkel, 1988) and small
217 tropical hibernators such as *Cheirogaleidae* and *Tenrecidae* species, which show a 70% reduction
218 (Dausmann et al., 2009; Wein, 2010). Thus, the ‘deep hibernator’ group includes the species capable
219 of reducing their total energy expenditure by about 90% or more during hibernation as compared to the
220 euthermic state and reaching a body temperature during torpor below 10°C (mainly small Holarctic
221 species; Heldmaier et al., 2004)

222 In addition, the analyses of Turbill et al. 2011 indicated a body mass threshold of 1.5 kg, below
223 which the benefits of hibernation (compared to non-hibernation) for longevity increased. To test the
224 effect of hibernation season duration on longevity between hibernators < 1.5kg and larger ones, we
225 used the data set excluding bats and hibernators > 1.5 kg.

226 Branch lengths for respective consensus trees were calculated with the ‘compute.brLen’ function
227 from the ‘ape’ package based on Grafen's (1989) computations, and were used to compute PGLS
228 models with the ‘caper’ package in R (see section 2.5 below).

229

230 2.5 Statistics

231

232 We tested for a significant relationship between hibernation season duration and species
233 maximum longevity, using phylogenetic generalized least squares (PGLS) models using the ‘ape 5.0’,
234 ‘apTreeshape 1.5’ and ‘caper 1.0’ packages in R v. 3.6.2 (Orme et al., 2013; Paradis, 2011; Paradis and
235 Schliep, 2019; R Core Team 2014). We thus statistically “controlled” for the influence of the
236 phylogenetic relationships among species on the variables before evaluating relationships. In addition,
237 the relative effect of the phylogenetic tree on the linear model could be estimated as a λ parameter,
238 ranging between 0 (covariation among species measurements is independent of co-ancestry) and 1
239 (covariance entirely explained by co-ancestry). Testing the models with $\lambda = 0$ allowed comparison to
240 λ -positive models, and thus the extent to which phylogeny influenced analyses of the models examined.
241 In addition to phylogeny, our model evaluated the influences of average body mass (of adults) of the
242 different species, bats and arboreality lifestyle, and the fact that some data were acquired from captive
243 and wild populations (see below).

244 We ran PGLS models for the 4 different conditions listed above (Table 1). Longevity was our
245 dependent variable in all models, and hibernation season duration and species average body mass were
246 independent variables. In all models, body mass and longevity were log-transformed to normalize their
247 distributions, and all independent variables were standardized (using *z-scores*), so that their coefficients
248 are directly comparable as estimates of effect sizes (Abdi, 2007). In the original models, we included

Time dimension of allocation trade-offs in hibernators

249 the interaction *hibernation season duration x body mass* to test for the possibility that the effect of
250 hibernation season duration on longevity was more important for species of small body mass (see Fig
251 2 in Turbill et al., 2011), as well as a 'captive/wild' factor to account for captivity-related variation in
252 longevity (Tidière et al., 2016). However, these factors were parsimoniously dropped in the final
253 models based on Akaike's Information Criterion (AIC). Among the models within $\Delta AIC < 2$
254 ($\Delta AIC_i = AIC_i - AIC_{\min}$), we kept the model with the lowest number of terms (see Electronic
255 Supplementary Materials Table S3). Nevertheless, body mass was retained throughout our models,
256 because of the dominance that it shows as a primary axis of energetics and life history (Brown et al.,
257 2004; Stearns, 1992). In order to control for higher longevity due to particular lifestyles, we added a
258 'bat (yes/no)' factor in the full model (Turbill et al., 2011; Wilkinson and South, 2002) and an
259 'arboreality (yes/no)' factor in each model (Healy et al., 2014; Kamilar et al., 2010; Shattuck and
260 Williams, 2010). We limited the number of additional predictors in order to maintain sufficient
261 statistical power with respect to the sample size (table 2 ; Mundry, 2014).

262 For the final models, the level of covariation in maximum longevity among species was
263 estimated by maximum likelihood (λ_{ML}).

264 Within bats (individuals from wild populations only), we were not able to estimate the effects of
265 body mass and hibernation season duration on longevity, while controlling statistically for phylogeny.
266 We had too few species of bats ($N = 27$; Münkemüller et al., 2013) for properly evaluating the
267 phylogenetic signal (the lower CI bound for the phylogenetic signal could not be estimated; see
268 Electronic Supplementary Material, Fig S2). Thus, we present simple linear regressions for this group
269 later indicated as model 5 (Table 1 and 2).

270

271

272 3 Results

273 The characteristics of the models and data used are summarized in Table 1. For each model,
274 hibernation season duration and longevity were similar in range between the different datasets (Table
275 1). Naturally, the range of body mass was much smaller when considering only deep hibernators, small
276 species and bats.

277 **Model 1 (N = 82):** Accounting for the effect of phylogeny, variation in longevity was positively
278 associated with hibernation season duration and body mass across all hibernating mammals (Table 2,
279 Fig 1 and 2). On average, bats had significantly longer lifespans (79%, $\bar{x} = 21$ years, N = 27) as well
280 as species with an arboreal lifestyle (11%, $\bar{x} = 13$ years, N = 16), than other mammals ($\bar{x} = 11.8$ years,
281 N = 55) (Table 2).

282 **Model 2 (N = 55):** Removing hibernating bats from the analyses showed that hibernation season
283 duration had a significant positive effect on longevity (Table 2, Fig 1 and 2). The positive effect of
284 body mass and an arboreal lifestyle on longevity remained, mammals with a higher body mass or an
285 arboreal lifestyle exhibiting significantly longer lifespan (Table 2, Fig 1 and 2).

286 **Models 3 and 4 (N = 46 and N = 44 respectively):** When only deep hibernators (model 3) and
287 small hibernators < 1.5 kg (excluding bats) were considered (model 4), we found a positive effect of
288 hibernation season duration on longevity (Table 2, Fig 1 and 2). The positive effect of arboreality
289 lifestyle on longevity only remained for small hibernators (model 4).

290 Among the above models, the effect of hibernation season duration was slightly higher for small
291 hibernators < 1.5 kg and highly significant (Table 2, Fig 1 and 2). These models showed a strong
292 influence of phylogeny on the results (Table 2). Ignoring the effect of phylogeny by constraining λ to
293 0 removed the effect of hibernation season duration on longevity (Table 2).

294 **Model 5** ($N = 27$): Because our sample size for bats alone was too small, we could not perform
295 an analysis controlling for phylogeny. Instead, we ran simple linear models to test for the effects of
296 hibernation season duration and body mass on longevity. Here as well, hibernation season duration,
297 but not body mass, was positively and significantly related to maximum longevity (Table 2, Fig 1 and
298 2). Hibernation season duration had an effect on bat longevity up to two times higher than in previous
299 models excluding bats. This significant effect without accounting for phylogeny was probably due to
300 a lower level of phylogenetic differences among bat species, compared to other models including up
301 to eight different orders.

302

303 4 Discussion

304 4.1 Influence hibernation season duration on longevity

305

306 Our purpose was to examine the extent to which the activity time budget explains variation in
307 life history traits in mammals. We investigated this question in hibernating species because of their
308 marked seasonal cycle of activity/inactivity, which is associated with very different risks of mortality
309 (Turbill et al., 2011). While controlling for phylogeny, our study highlighted a positive influence of
310 hibernation season duration on longevity in mammalian hibernators. These results were in agreement
311 with an early study that tested the effect of hibernation duration on longevity in captive Turkish
312 hamsters (Lyman et al., 1981). In agreement with Dobson (2007) and Sibly and Brown (2007), the two
313 major axes of life histories of mammalian hibernators are body mass and lifestyle, with lifestyle
314 contributing to the slow-fast continuum. The bat lifestyle (e.g. aerial) had the greatest influence on
315 longevity, with a positive effect on longevity that was three times greater than the arboreality lifestyle.
316 The effect of hibernation season duration, in addition to these lifestyles, appeared to be roughly one-
317 third of the effect of body mass on longevity (see model estimates in Table 2).

Time dimension of allocation trade-offs in hibernators

318 Our results show that the effects of hibernation season duration on longevity were consistent
319 across a wide range of body sizes, and became stronger with the limitation in body mass to small
320 species (species < 1.5 kg), especially for bats (Figure 1) . Interestingly, hibernation season duration
321 appeared to be more important than body mass in explaining longevity in the latter species. These
322 results support the idea that hibernation (1) is an efficient strategy that limits mortality in periods of
323 energy scarcity for some larger species facing strong energy constraints during part of the year (e.g.,
324 *Marmota* species), and (2) may be an especially effective strategy for small mammals that are expected
325 to suffer from both higher predation rate (Cohen et al., 1993; Sinclair et al., 2003), and increased loss
326 of energy expenditure during winter (Ruf and Geiser, 2015). In either case, increased hibernation season
327 duration may increase both annual survival rates (Turbill et al., 2016) and overall longevity. Note that
328 in some cases, the lack of relationship between body mass and longevity in our study could also be due
329 to a smaller range of body mass variation than reported in other studies (for instance in bats; Wilkinson
330 and South, 2002).

331 In our study, the effect of hibernation season duration on the longevity for bats was twice that of
332 small non-flying terrestrial mammals, though this result should be considered with caution since we
333 were not able to control for phylogeny when considering only bats (Table 2, Fig 2 and 3). Bats stand
334 somewhat apart from other mammals, distinguished notably by their ability for sustained flight, an
335 important lifestyle characteristic (Sibly and Brown, 2007). Flying is an energy-intensive activity,
336 considerably more than terrestrial locomotion (Thomas and Suthers, 1972; Tucker, 1968). Thomas and
337 Suthers (1972) estimated that the greater spear-nosed bat (*Phyllostomus hastatus*) increases its resting
338 metabolic rate more than 34 times during flight, while rodents of similar size increase it only by 8-fold
339 during terrestrial locomotion. Thus, in bats the reduction of metabolism during hibernation is
340 particularly important compared to their period of activity (Wilkinson and South, 2002).

Time dimension of allocation trade-offs in hibernators

341 The marked effect of hibernation season duration on longevity in bats may also be explained by
342 some extreme physiological adaptations to hibernation having evolved in response to specific
343 ecological and anatomical constraints (Willis, 2017). For instance, several bat species are capable of
344 very long torpor bouts (up to 60 days; reviewed in Ruf and Geiser 2015), perhaps in response to their
345 limitation on accumulation of internal or external energy reserves (Willis, 2017). In addition, the little
346 brown bat (*Myotis lucifugus*), for instance, is capable of performing "heterothermic arousals",
347 corresponding to shallow torpor bouts ($T_{\text{skin}} > 20^{\circ}\text{C}$), during arousal phases, and thus reduce the cost
348 of euthermia (Czenze et al., 2017; Jonasson and Willis, 2012). This particular adaptation may be
349 present in other bat species as well. Finally, bats are highly gregarious during hibernation and can
350 cluster in colonies of up to thousands of individuals (Clawson et al., 1980). Huddling could enable
351 them to reduce energy costs and water loss during hibernation, making hibernation a particularly
352 profitable strategy (Boratyński et al., 2012, 2015; Boyles et al., 2008; Gilbert et al., 2010).

353 Comparisons between of models either including (model 2) or excluding (model 3) species with
354 lowest metabolic reduction during hibernation did not reveal significant differences. These results
355 suggest that the effect of hibernation season duration on longevity remains consistent whatever the rate
356 of metabolic reduction reached during hibernation compared to the active state (between 70 to 90%).
357 This finding should pave the way for future studies to specifically test this effect of metabolic reduction
358 during hibernation.

359 Interestingly, in all PGLS models, removing the effect of phylogeny by constraining λ to 0 also
360 removed the effect of hibernation season duration on longevity. This suggests that the effect of
361 hibernation season duration on longevity is masked by the phylogenetic pattern. Thus, hibernation
362 season duration might be a stronger explanation of variation within species or between closely related
363 species, as shown in Turkish hamsters (Lyman et al., 1981). For instance, studies comparing

Time dimension of allocation trade-offs in hibernators

364 populations of golden-mantled ground squirrels (*Callospermophilus lateralis*) and Columbian ground
365 squirrels (*Uroditellus columbianus*) living along an altitudinal gradient show that populations with
366 longer hibernation season duration generally have higher annual survival and longevity (Bronson,
367 1979; Dobson and Murie, 1987; Murie and Harris, 1982).

368 Although our results highlight an association between hibernation season duration and longevity,
369 they do not provide a causal mechanism through which such an association might arise. Periods of
370 prolonged inactivity are likely to increase longevity through the integration of multiple factors affecting
371 both intrinsic and extrinsic mortality, as discussed below.

372

373 4.2 Factors affecting extrinsic and intrinsic mortality and the evolution of hibernation

374

375 Energetic stress, when energy demand is greater than energy availability in the environment, has
376 a proximate role in the regulation of hibernation pattern (Vuarin and Henry, 2014). However, few
377 studies have focused on the causal link between energetic stress, and the timing of hibernation
378 immergence and emergence (e.g., Humphries et al., 2002). Thus, the hypothesis that hibernation occurs
379 primarily as a response to an energetic stress has not been completely studied (focusing on torpor bouts
380 frequency, depth and duration). To the best of our knowledge, the only study having measured both
381 energy availability in the environment and individual energy expenditure before immergence in
382 hibernation shows in eastern chipmunks (*Tamias striatus*), that immergence occurs while food is still
383 plentiful and climatic conditions are still favorable for maximizing energy storage (Humphries et al.,
384 2002). Other observations also suggest that immergence into hibernation while food is still available
385 seems common, at least in sciurids (Humphries et al., 2003) and for the little pocket mouse (French,

Time dimension of allocation trade-offs in hibernators

2004). Thus, food availability and ambient temperature alone may not be sufficient to explain the phenology of immergence.

Other evidence suggests that hibernation is not initiated solely in response to deficiencies in energy, water, or poor food quality. Many observations suggest that early immergence (before energetically stressful periods start) occurs when the benefits of reproduction are low. For instance, in years of low beech seed abundance, the edible dormouse (*Glis glis*) skips reproduction, quickly accumulates fat reserves, and is able to hibernate for up to 11 months (Hoelzl et al., 2015). This occurs even if food in the environment is sufficient to allow the edible dormouse to remain active but not to reproduce. Similarly, Eastern chipmunks skip reproduction and cease foraging for almost a full year when food availability is particularly low (Munro et al., 2008). It seems that at that time, chipmunks rely on large amounts of food hoarded during the preceding year; but there is no evidence of torpor expression. This kind of behaviour is also observed in several hibernating ground squirrel species. Females that fail to reproduce may immerge up to several weeks before the others (Bintz, 1988; Choromanski-Norris et al., 1986; Michener, 1978; Neuhaus, 2000). An experiment in semi-natural conditions shows that female European ground squirrels (*Spermophilus citellus*) that were separated from males (and thus did not breed) entered into hibernation 4 to 6 weeks before females that were not separated (Millesi et al., 2008). These results support the view that hibernation phenology is influenced by a trade-off between reproduction and survival, where hibernation seems to provide benefits other than surviving periods of energetic stress. This trade-off may also explain differences (up to 1 month) in the timing of immergence and emergence between gender and age observed in rodents (Siutz et al., 2016; Sheriff et al., 2011; Kawamichi, 1989 ; Kart Gür and Gür, 2015; Snyder et al., 1961; Holekamp and Nunes, 1989) and bats (Decher and Choate, 1995; Norquay and Willis, 2014; Stebbings, 1970; Thomson, 1982).

Time dimension of allocation trade-offs in hibernators

409 So far, most studies have focused mainly on temperate hibernating species. However heterothermy
410 that occurs during daily torpor and hibernation, is taxonomically and geographically widespread (Ruf
411 and Geiser, 2015). A surprisingly large proportion of mammals, including a monotreme, several
412 marsupials, and placental species regularly enter daily torpor and seasonal hibernation in the southern
413 hemisphere (Grigg and Beard, 2000). For some species in these regions, the use of torpor may not be
414 related to low environmental temperatures or limited food availability (Nowack et al, 2020). For
415 example, the short-beaked echidna hibernates (Grigg et al., 1989) while ants and termites, which
416 constitute the main part of its diet, remain available throughout the year (Grigg and Beard, 2000).
417 Short-beaked echidnas are heavily armored, perhaps rendering avoidance of predation an unlikely
418 adaptive benefit for hibernation. These observations suggest that some species may use hibernation
419 because of the energy advantages provided by lack of activity, even though it is not an energy necessity
420 for survival during a period of energetic stress (Grigg and Beard, 2000). Such case studies broaden the
421 scope of possibilities for understanding the evolution of hibernation (Grigg and Beard, 2000; Ruf et
422 al., 2012), and open up exciting perspectives for future research.

423

424 5 Conclusion

425 Hibernation is considered an adaptation to seasonal, hence predictable decrease in food resources
426 and ambient temperatures. However, hibernation is also observed in mild climates and when ambient
427 conditions are still favorable for activity (Nowack et al., 2020). If remarkable physiological aspects of
428 hibernation have been widely studied, fewer studies have focused on its ecological and evolutionary
429 significance in the field. Our study provides evidence that there may be a relationship between activity
430 time budgets, and hence the time dimension of allocation trade-off, and life history traits.

431 Our phylogenetic analyses shows that variations in hibernation season duration can partially
432 explain variations in longevity in hibernators. The models show a strong influence of phylogeny on
433 this relationship and highlight the need for in-depth studies at an inter- and intra-population scales. For
434 example, future studies may attempt to consider activity time budgets in the context of the pace of life
435 syndrome by examining variations in hibernation with other physiological and behavioral traits. Our
436 results, combined with information available in the literature, suggest that, in addition to its survival
437 benefits during a period of energetic stress, hibernation season duration may have evolved to reduce
438 the effects of other sources of extrinsic and intrinsic mortality.

439

440 6 Conflict of Interest

441 *The authors declare that the research was conducted in the absence of any commercial or financial*
442 *relationships that could be construed as a potential conflict of interest.*

443 7 Author Contributions

444 T.C.: conception and drafting the manuscript

445 S.G., C.H.: development of the concept and writing of the manuscript

446 T.C.: data collection

447 T.C., V.A.V., F.S.D.: data analyses

448 V.A.V., M.L.T., P.B., F.S.D., C.H., S.G.: substantial contributions to the conception

449 F.S.D.: English composition with many revisions of the text

450 All authors contributed to the revisions.

451 8 Acknowledgments

452 The authors are grateful to François Criscuolo for his help in the phylogenetic analyses. Two
453 anonymous reviewers provided excellent suggestions for analysis and manuscript improvements.

454 F.S.D. thanks the Institute of Advanced Studies of the University of Strasbourg for their financial
455 support through an USIAS fellowship, and the Région Grand Est and the Eurométropole de Strasbourg

456 for the award of a Gutenberg Excellence Chair during the writing of this project. S.G. was financially
457 supported by the Austrian Science Fund (FWF) (Grant no. P31577-B25).

458 9 References

- 459 Abdi, H. (2007). Z-scores. *Encycl. Meas. Stat.* 3, 1055–1058.
- 460 Alonso-Alvarez, C., Bertrand, S., Devevey, G., Prost, J., Faivre, B., and Sorci, G. (2004). Increased
461 susceptibility to oxidative stress as a proximate cost of reproduction. *Ecol. Lett.* 7, 363–368.
- 462 Amstrup, S.C., and DeMaster, D.P. (2003). Polar bear, *Ursus maritimus*. *Wild Mamm. N. Am. Biol.*
463 *Manag. Conserv.* 2, 587–610.
- 464 Austad, S.N., and Fischer, K.E. (1991). Mammalian Aging, Metabolism, and Ecology: Evidence
465 From the Bats and Marsupials. *J. Gerontol.* 46, B47–B53.
- 466 Bielby, J., Mace, G.M., Bininda-Emonds, O.R.P., Cardillo, M., Gittleman, J.L., Jones, K.E., Orme,
467 C.D.L., and Purvis, A. (2007). The Fast-Slow Continuum in Mammalian Life History: An Empirical
468 Reevaluation. *Am. Nat.* 169, 748–757.
- 469 Bintz, G.L. (1988). Lipid synthesis and deposition by adult Richardson’s ground squirrels in the
470 natural environment. *J. Comp. Physiol. B* 158, 199–204.
- 471 Blanco, M.A., and Sherman, P.W. (2005). Maximum longevity of chemically protected and non-
472 protected fishes, reptiles, and amphibians support evolutionary hypotheses of aging. *Mech. Ageing*
473 *Dev.* 126, 794–803.
- 474 Blueweiss, L., Fox, H., Kudzma, V., Nakashima, D., Peters, R., and Sams, S. (1978). Relationships
475 between body size and some life history parameters. *Oecologia* 37, 257–272.
- 476 Boratyński, J.S., Rusiński, M., Kokurewicz, T., Bereszyński, A., and Wojciechowski, M.S. (2012).
477 Clustering behavior in wintering greater mouse-eared bats *Myotis myotis* - the effect of micro-
478 environmental conditions.
- 479 Boratyński, J.S., Willis, C.K.R., Jefimow, M., and Wojciechowski, M.S. (2015). Huddling reduces
480 evaporative water loss in torpid Natterer’s bats, *Myotis nattereri*. *Comp. Biochem. Physiol. A. Mol.*
481 *Integr. Physiol.* 179, 125–132.
- 482 Boyles, J.G., Storm, J.J., and Brack, V. (2008). Thermal Benefits of Clustering during Hibernation: A
483 Field Test of Competing Hypotheses on *Myotis sodalis*. *Funct. Ecol.* 22, 632–636.
- 484 Bright, P.W., Balmforth, Z., and Macpherson, J.L. (2015). The effect of changes in traffic flow on
485 mammal road kill counts. *Appl. Ecol. Environ. Res.* 13, 171–179.
- 486 Bronson, M.T. (1979). Altitudinal Variation in the Life History of the Golden-Mantled Ground
487 Squirrel (*Spermophilus lateralis*). *Ecology* 60, 272–279.

Time dimension of allocation trade-offs in hibernators

- 488 Brown, J.H., Gilgooly, J.F., Allen, A.P., Savage, V.M., and West, G.B. (2004). Toward a Metabolic
489 Theory of Ecology. *Ecology* 85, 1771–1789.
- 490 Choromanski-Norris, J., Fritzell, E.K., and Sargeant, A.B. (1986). Seasonal Activity Cycle and
491 Weight Changes of the Franklin's Ground Squirrel. *Am. Midl. Nat.* 116, 101.
- 492 Clawson, R.L., LaVal, R.K., LaVal, M.L., and Caire, W. (1980). Clustering Behavior of Hibernating
493 *Myotis sodalis* in Missouri. *J. Mammal.* 61, 245–253.
- 494 Cohen, J.E., Pimm, S.L., Yodzis, P., and Saldaña, J. (1993). Body Sizes of Animal Predators and
495 Animal Prey in Food Webs. *J. Anim. Ecol.* 62, 67–78.
- 496 Czenze, Z.J., Jonasson, K.A., and Willis, C.K.R. (2017). Thrifty Females, Frisky Males: Winter
497 Energetics of Hibernating Bats from a Cold Climate. *Physiol. Biochem. Zool.* 90, 502–511.
- 498 Dausmann, K.H., Glos, J., and Heldmaier, G. (2009). Energetics of tropical hibernation. *J. Comp.*
499 *Physiol. B* 179, 345–357.
- 500 Decher, J., and Choate, J.R. (1995). *Myotis grisescens*. *Mamm. Species* 1–7.
- 501 Dobson, F.S. (2007). A lifestyle view of life-history evolution. *Proceedings of the National Academy*
502 *of Science* 104, 17565.
- 503 Dobson, F.S., and Murie, J.O. (1987). Interpretation of intraspecific life history patterns: evidence
504 from Columbian ground squirrels. *The American Naturalist* 129, 382–397.
- 505 Dobson, F.S., and Oli, M.K. (2007). Fast and slow life histories of mammals. *Écoscience* 14, 292–
506 299.
- 507 French, Alan.R. (2004). Factors Influencing the Timing of Dormancy in the Pocket Mouse,
508 *Perognathus longimembris*. 93.
- 509 Geiser, F., and Körtner, G. (2010). Hibernation and daily torpor in Australian mammals. *Aust. Zool.*
510 35, 204–215.
- 511 Gilbert, C., McCafferty, D., Maho, Y.L., Martrette, J.-M., Giroud, S., Blanc, S., and Ancel, A.
512 (2010). One for all and all for one: the energetic benefits of huddling in endotherms. *Biol. Rev.* 85,
513 545–569.
- 514 Grafen, A. (1989). The phylogenetic regression. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 326, 119–
515 157.
- 516 Grigg, G., and Beard, L. (2000). Hibernation by Echidnas in Mild Climates: Hints about the
517 Evolution of Endothermy? In *Life in the Cold*, G. Heldmaier, and M. Klingenspor, eds. (Springer
518 Berlin Heidelberg), pp. 5–19.
- 519 Grigg, G.C., Beard, L.A., and Augee, M.L. (1989). Hibernation in a monotreme, the echidna
520 (*Tachyglossus aculeatus*). *Comp. Biochem. Physiol. A Physiol.* 92, 609–612.

Time dimension of allocation trade-offs in hibernators

- 521 Gummer, D.L. (2005). Geographic variation in torpor patterns: the northernmost prairie dogs and
522 kangaroo rats. PhD Thesis.
- 523 Healy, K. (2015). Eusociality but not fossoriality drives longevity in small mammals. Proc. R. Soc. B
524 Biol. Sci. 282, 20142917.
- 525 Healy, K., Guillerme, T., Finlay, S., Kane, A., Kelly, S.B.A., McClean, D., Kelly, D.J., Donohue, I.,
526 Jackson, A.L., and Cooper, N. (2014). Ecology and mode-of-life explain lifespan variation in birds
527 and mammals. Proc. R. Soc. B Biol. Sci. 281, 20140298.
- 528 Healy, K., Ezard, T.H.G., Jones, O.R., Salguero-Gómez, R., and Buckley, Y.M. (2019). Animal life
529 history is shaped by the pace of life and the distribution of age-specific mortality and reproduction.
530 Nat. Ecol. Evol. 3, 1217–1224.
- 531 Heldmaier, G., Ortmann, S., and Elvert, R. (2004). Natural hypometabolism during hibernation and
532 daily torpor in mammals. Respir. Physiol. Neurobiol. 141, 317–329.
- 533 Hellgren, E.C. (1998). Physiology of Hibernation in Bears. *Ursus* 10, 467–477.
- 534 Heppell, S.S., Caswell, H., and Crowder, L.B. (2000). Life Histories and Elasticity Patterns:
535 Perturbation Analysis for Species with Minimal Demographic Data. Ecology 81, 654–665.
- 536 Hidasi-Neto, J., Loyola, R., and Cianciaruso, M.V. (2015). Global and local evolutionary and
537 ecological distinctiveness of terrestrial mammals: identifying priorities across scales. Divers. Distrib.
538 21, 548–559.
- 539 Hirshfield, M.F., and Tinkle, D.W. (1975). Natural selection and the evolution of reproductive effort.
540 Proc. Natl. Acad. Sci. 72, 2227–2231.
- 541 Hoelzl, F., Bieber, C., Cornils, J.S., Gerritsmann, H., Stalder, G.L., Walzer, C., and Ruf, T. (2015).
542 How to spend the summer? Free-living dormice (*Glis glis*) can hibernate for 11 months in non-
543 reproductive years. J. Comp. Physiol. B 185, 931–939.
- 544 Holekamp, K.E., and Nunes, S. (1989). Seasonal variation in body weight, fat, and behavior of
545 California ground squirrels (*Spermophilus beecheyi*). Can. J. Zool. 67, 1425–1433.
- 546 Holmes, D.J., and Austad, S.N. (1994). Fly Now, Die Later: Life-History Correlates of Gliding and
547 Flying in Mammals. J. Mammal. 75, 224–226.
- 548 Humphries, M.M., Thomas, D.W., Hall, C.L., Speakman, J.R., and Kramer, D.L. (2002). The
549 energetics of autumn mast hoarding in eastern chipmunks. Oecologia 133, 30–37.
- 550 Humphries, M.M., Thomas, D.W., and Kramer, D.L. (2003). The Role of Energy Availability in
551 Mammalian Hibernation: A Cost-Benefit Approach. Physiological and Biochemical Zoology 76,
552 165–179.
- 553 Jeschke, J.M., and Kokko, H. (2009). The roles of body size and phylogeny in fast and slow life
554 histories. Evol. Ecol. 23, 867–878.

Time dimension of allocation trade-offs in hibernators

- 555 Jonasson, K.A., and Willis, C.K.R. (2012). Hibernation energetics of free-ranging little brown bats. *J.*
556 *Exp. Biol.* *215*, 2141–2149.
- 557 Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L., Safi, K., Sechrest, W.,
558 Boakes, E.H., Carbone, C., et al. (2009). PanTHERIA: a species-level database of life history,
559 ecology, and geography of extant and recently extinct mammals. *Ecology* *90*, 2648–2648.
- 560 Jones, O.R., Gaillard, J.-M., Tuljapurkar, S., Alho, J.S., Armitage, K.B., Becker, P.H., Bize, P.,
561 Brommer, J., Charmantier, A., Charpentier, M., et al. (2008). Senescence rates are determined by
562 ranking on the fast–slow life-history continuum. *Ecol. Lett.* *11*, 664–673.
- 563 Kamilar, J.M., Bribiescas, R.G., and Bradley, B.J. (2010). Is group size related to longevity in
564 mammals? *Biology Letters* *6*, 736–739.
- 565 Kart Gür, M., and Gür, H. (2015). Age and sex differences in hibernation patterns in free-living
566 Anatolian ground squirrels. *Mamm. Biol.* *80*, 265–272.
- 567 Kawamichi, M. (1989). Nest Structure Dynamics and Seasonal Use of Nests by Siberian Chipmunks
568 (*Eutamias sibiricus*). *J. Mammal.* *70*, 44–57.
- 569 Kenagy, G.J., and Bartholomew, G.A. (1985). Seasonal Reproductive Patterns in Five Coexisting
570 California Desert Rodent Species: Ecological Archives M055-002. *Ecol. Monogr.* *55*, 371–397.
- 571 Lack, D.L. (1966). Population studies of birds (Clarendon P.).
- 572 Lehmer, E.M., Savage, L.T., Antolin, M.F., and Biggins, D.E. (2006). Extreme plasticity in
573 thermoregulatory behaviors of free-ranging black-tailed prairie dogs. *Physiol. Biochem. Zool.* *79*,
574 454–467.
- 575 Lewis, K.N., Andziak, B., Yang, T., and Buffenstein, R. (2013). The naked mole-rat response to
576 oxidative stress: just deal with it. *Antioxid. Redox Signal.* *19*, 1388–1399.
- 577 Lovegrove, B.G., Raman, J., and Perrin, M.R. (2001). Heterothermy in elephant shrews,
578 *Elephantulus spp.*(Macroscelidea): daily torpor or hibernation? *J. Comp. Physiol. B* *171*, 1–10.
- 579 Lyman, C.P., O'Brien, R.C., Greene, G.C., and Papafrangos, E.D. (1981). Hibernation and longevity
580 in the Turkish hamster *Mesocricetus brandti*. *Science* *212*, 668–670.
- 581 MacRae, S.L., Croken, M.M., Calder, R.B., Aliper, A., Milholland, B., White, R.R., Zhavoronkov,
582 A., Gladyshev, V.N., Seluanov, A., Gorbunova, V., et al. (2015). DNA repair in species with extreme
583 lifespan differences. *Aging* *7*, 1171–1182.
- 584 Magalhães, J.P.D., and Costa, J. (2009). A database of vertebrate longevity records and their relation
585 to other life-history traits. *J. Evol. Biol.* *22*, 1770–1774.
- 586 Magnhagen, C. (1991). Predation risk as a cost of reproduction. *Trends Ecol. Evol.* *6*, 183–186.
- 587 Martin, T.E. (2015). Age-related mortality explains life history strategies of tropical and temperate
588 songbirds. *Science* *349*, 966–970.

Time dimension of allocation trade-offs in hibernators

- 589 Masoro, E.J. (2006). Caloric Restriction and Aging: Controversial Issues. *J. Gerontol. Ser. A* 61, 14–
590 19.
- 591 Michener, G.R. (1978). Effect of age and parity on weight gain and entry into hibernation in
592 Richardson's ground squirrels. *Can. J. Zool.* 56, 2573–2577.
- 593 Millesi, E., Divjak, A., and Strauss, A. (2008). Seasonal timing and pre-hibernation fattening in
594 breeding and non-breeding European ground squirrels. *Hypometabolism Anim. Hibernation Torpor*
595 *Cryobiol. Univ. KwaZulu-Natal Pietermaritzbg.* 289–294.
- 596 Morris, P.A., and Morris, M.J. (1988). Distribution and abundance of hedgehogs (*Erinaceus*
597 *europaeus*) on New Zealand roads. *N. Z. J. Zool.* 15, 491–498.
- 598 Mundry, R. (2014). Statistical issues and assumptions of phylogenetic generalized least squares. In
599 *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology*,
600 (Springer), pp. 131–153.
- 601 Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffrers, K., and Thuiller, W.
602 (2013). How to measure and test phylogenetic signal. *Methods Ecol. Evol.* 743–756.
- 603 Munro, D., Thomas, D.W., and Humphries, M.M. (2008). Extreme suppression of aboveground
604 activity by a food-storing hibernator, the eastern chipmunk (*Tamias striatus*). *Can. J. Zool.* 86, 364–
605 370.
- 606 Munshi-South, J., and Wilkinson, G.S. (2010). Bats and birds: Exceptional longevity despite high
607 metabolic rates. *Ageing Res. Rev.* 9, 12–19.
- 608 Murie, J.O., and Harris, M.A. (1982). Annual Variation of Spring Emergence and Breeding in
609 Columbian Ground Squirrels (*Spermophilus columbianus*). *J. Mammal.* 63, 431–439.
- 610 Neuhaus, P. (2000). Timing of Hibernation and Molt in Female Columbian Ground Squirrels. *J.*
611 *Mammal.* 81, 571–577.
- 612 Norquay, K.J.O., and Willis, C.K.R. (2014). Hibernation phenology of *Myotis lucifugus*. *J. Zool.* 294,
613 85–92.
- 614 Nowack, J., Levesque, D.L., Reher, S., and Dausmann, K.H. (2020). Variable climates lead to
615 varying phenotypes: 'weird' mammalian torpor and lessons from non-Holarctic species. *Front. Ecol.*
616 *Evol.* 8.
- 617 Oli, M.K. (2004). The fast–slow continuum and mammalian life-history patterns: an empirical
618 evaluation. *Basic Appl. Ecol.* 5, 449–463.
- 619 Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., and Fritz, S. (2013). The caper package:
620 comparative analysis of phylogenetics and evolution in R. *R Package Version 5*, 1–36.
- 621 Paradis, E. (2011). *Analysis of Phylogenetics and Evolution with R* (Springer Science & Business
622 Media).

Time dimension of allocation trade-offs in hibernators

- 623 Paradis, E., and Schliep, K. (2019). ape 5.0: an environment for modern phylogenetics and
624 evolutionary analyses in R. *Bioinformatics* 35, 526–528.
- 625 Promislow, D.E.L., and Harvey, P.H. (1990). Living fast and dying young: A comparative analysis of
626 life-history variation among mammals. *J. Zool.* 220, 417–437.
- 627 Reznick, D. (1985). Costs of Reproduction: An Evaluation of the Empirical Evidence. *Oikos* 44,
628 257–267.
- 629 Ruf, T., and Geiser, F. (2015). Daily torpor and hibernation in birds and mammals. *Biol. Rev.* 90,
630 891–926.
- 631 Ruf, T., Bieber, C., and Turbill, C. (2012). Survival, Aging, and Life-History Tactics in Mammalian
632 Hibernators. In *Living in a Seasonal World: Thermoregulatory and Metabolic Adaptations*, T. Ruf, C.
633 Bieber, W. Arnold, and E. Millesi, eds. (Berlin, Heidelberg: Springer Berlin Heidelberg), pp. 123–
634 132.
- 635 Shanley, D.P., and Kirkwood, T.B.L. (2000). Calorie Restriction and Aging: A Life-History
636 Analysis. *Evolution* 54, 740–750.
- 637 Shattuck, M.R., and Williams, S.A. (2010). Arboreality has allowed for the evolution of increased
638 longevity in mammals. *Proc. Natl. Acad. Sci.* 107, 4635–4639.
- 639 Sheriff, M.J., Kenagy, G.J., Richter, M., Lee, T., Tøien, Ø., Kohl, F., Buck, C.L., and Barnes, B.M.
640 (2011). Phenological variation in annual timing of hibernation and breeding in nearby populations of
641 Arctic ground squirrels. *Proc. R. Soc. B Biol. Sci.* 278, 2369–2375.
- 642 Sibly, R.M., and Brown, J.H. (2007). Effects of body size and lifestyle on evolution of mammal life
643 histories. *Proceedings of the National Academy of Sciences* 104, 17707–17712.
- 644 Sinclair, A.R.E., Mduma, S., and Brashares, J.S. (2003). Patterns of predation in a diverse predator–
645 prey system. *Nature* 425, 288–290.
- 646 Siutz, C., Franceschini, C., and Millesi, E. (2016). Sex and age differences in hibernation patterns of
647 common hamsters: adult females hibernate for shorter periods than males. *J. Comp. Physiol. B* 186,
648 801–811.
- 649 Snyder, R.L., Davis, D.E., and Christian, J.J. (1961). Seasonal Changes in the Weights of
650 Woodchucks. *J. Mammal.* 42, 297–312.
- 651 Speakman, J.R. (2005). Body size, energy metabolism and lifespan. *J. Exp. Biol.* 208, 1717–1730.
- 652 Stearns, S.C. (1992). The evolution of life histories.
- 653 Stebbings, R.E. (1970). A Comparative Study of *Plecotus Auritus* and *P. Austriacus* (Chiroptera,
654 *Vespertilionidae*) Inhabiting One Roost. *Bijdr. Tot Dierkd.* 40, 91–94.
- 655 Thomas, S.P., and Suthers, R.A. (1972). The Physiology and Energetics of Bat Flight. *J. Exp. Biol.*
656 57, 317–335.

Time dimension of allocation trade-offs in hibernators

- 657 Thomson, C.E. (1982). *Myotis sodalis*. Mamm. Species 1–5.
- 658 Tidière, M., Gaillard, J.-M., Berger, V., Müller, D.W.H., Lackey, L.B., Gimenez, O., Clauss, M., and
659 Lemaître, J.-F. (2016). Comparative analyses of longevity and senescence reveal variable survival
660 benefits of living in zoos across mammals. *Sci. Rep.* 6, 1–7.
- 661 Tøien, Ø., Blake, J., Edgar, D.M., Grahn, D.A., Heller, H.C., and Barnes, B.M. (2011). Hibernation
662 in Black Bears: Independence of Metabolic Suppression from Body Temperature. *Science* 331, 906–
663 909.
- 664 Tucker, V.A. (1968). Respiratory Exchange and Evaporative Water Loss in the Flying Budgerigar. *J.*
665 *Exp. Biol.* 48, 67–87.
- 666 Turbill, C., and Prior, S. (2016). Thermal climate-linked variation in annual survival rate of
667 hibernating rodents: shorter winter dormancy and lower survival in warmer climates. *Funct. Ecol.* 30,
668 1366–1372.
- 669 Turbill, C., Bieber, C., and Ruf, T. (2011). Hibernation is associated with increased survival and the
670 evolution of slow life histories among mammals. *Proc. R. Soc. B Biol. Sci.* 278, 3355–3363.
- 671 Turbill, C., Ruf, T., Smith, S., and Bieber, C. (2013). Seasonal variation in telomere length of a
672 hibernating rodent. *Biology Letters*.
- 673 Upham, N.S., Esselstyn, J.A., and Jetz, W. (2019). Inferring the mammal tree: Species-level sets of
674 phylogenies for questions in ecology, evolution, and conservation. *PLoS Biol.* 17.
- 675 Vuarin, P., and Henry, P.-Y. (2014). Field evidence for a proximate role of food shortage in the
676 regulation of hibernation and daily torpor: a review. *J. Comp. Physiol. B* 184, 683–697.
- 677 Walford, R.L., and Spindler, S.R. (1997). The Response to Calorie Restriction in Mammals Shows
678 Features Also Common to Hibernation: A Cross-Adaptation Hypothesis. *J. Gerontol. Ser. A* 52A,
679 B179–B183.
- 680 Watts, P.D., and Jonkel, C. (1988). Energetic Cost of Winter Dormancy in Grizzly Bear. *J. Wildl.*
681 *Manag.* 52, 654–656.
- 682 Wein, J. (2010). Effects of ambient temperature on tropical hibernation in the lesser hedgehog tenrec,
683 *Echinops telfairi*.
- 684 Wembridge, D.E., Newman, M.R., Bright, P.W., and Morris, P.A. (2016). An estimate of the annual
685 number of hedgehog (*Erinaceus europaeus*) road casualties in Great Britain. *Mammal Commun.* 2,
686 8–14.
- 687 Wilkinson, G.S., and South, J.M. (2002). Life history, ecology and longevity in bats. *Aging Cell* 1,
688 124–131.
- 689 Williams, G.C. (1966). Natural Selection, the Costs of Reproduction, and a Refinement of Lack's
690 Principle. *Am. Nat.* 100, 687–690.

Time dimension of allocation trade-offs in hibernators

691 Williams, C.T., Barnes, B.M., Kenagy, G.J., and Buck, C.L. (2014). Phenology of hibernation and
692 reproduction in ground squirrels: integration of environmental cues with endogenous programming.
693 *J. Zool.* 292, 112–124.

694 Willis, C.K.R. (2017). Trade-offs Influencing the Physiological Ecology of Hibernation in
695 Temperate-Zone Bats. *Integr. Comp. Biol.* 57, 1214–1224.

696 Wu, C.-W., and Storey, K.B. (2016). Life in the cold: links between mammalian hibernation and
697 longevity. *Biomol. Concepts* 7, 41–52.

698 Young, P.J. (1990). Hibernating patterns of free-ranging Columbian ground squirrels. *Oecologia* 83,
699 504–511.

700

701

702

In review

Time dimension of allocation trade-offs in hibernators

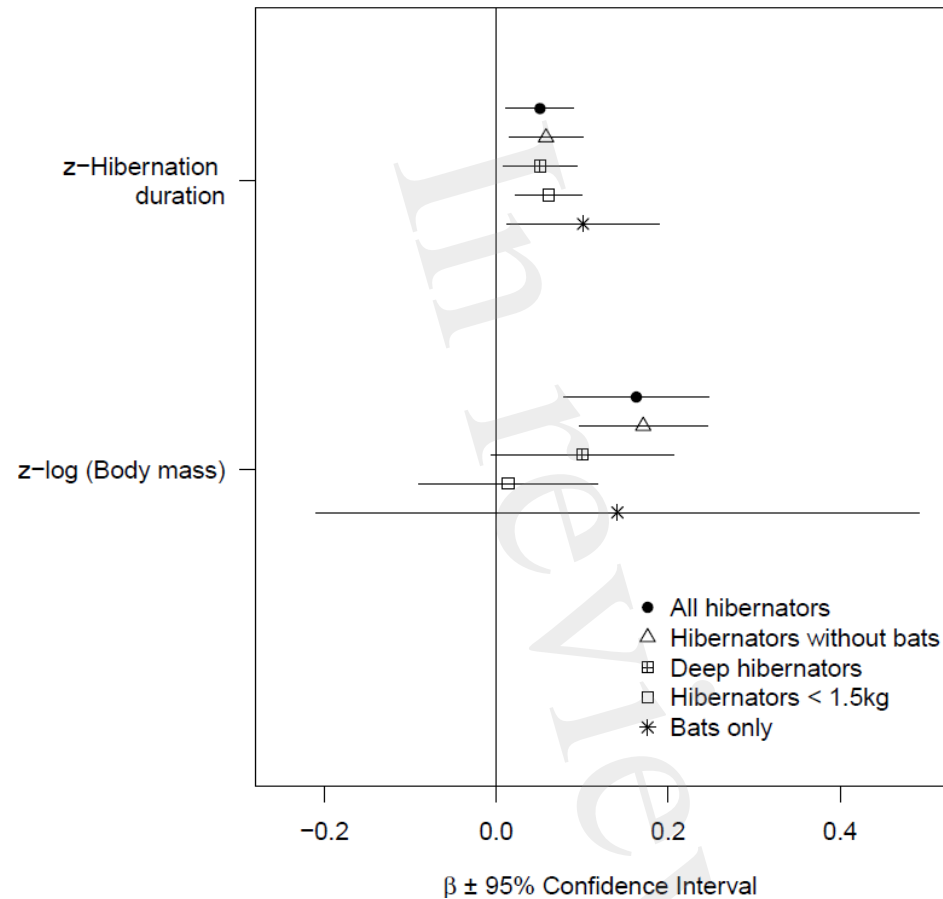
Model	1	2	3	4	5
Model type	PGLS	PGLS	PGLS	PGLS	Linear model
Hibernators > 1.5 kg	x	x			
Hibernators < 1.5 kg	x	x		x	
Deep hibernators	x	x	x		
Bats	x				x
Sample size	82	55	46	44	27
Arboreal and semi-arboreal species	16	16	11	15	0
Hibernation season duration range (day)	105-296	105-296	105-296	105-296	120-255
Longevity range (year)	3.5-49.5	3.5-49.5	3.5-49.5	3.5-29	6-41
Body mass range (g)	4.6-227500	8-227500	8-7300	8-958	4.6-28.55

Table 1. Summary of models and datasets. The category known as ‘deep hibernator’ includes the species capable of reducing their total energy expenditure by about 90% or more during hibernation as compared to the euthermic state and reaching a body temperature during torpor below 10°C (mainly small Holarctic species; Heldmaier et al., 2004). Crosses indicate group(s) included in each model.

Time dimension of allocation trade-offs in hibernators

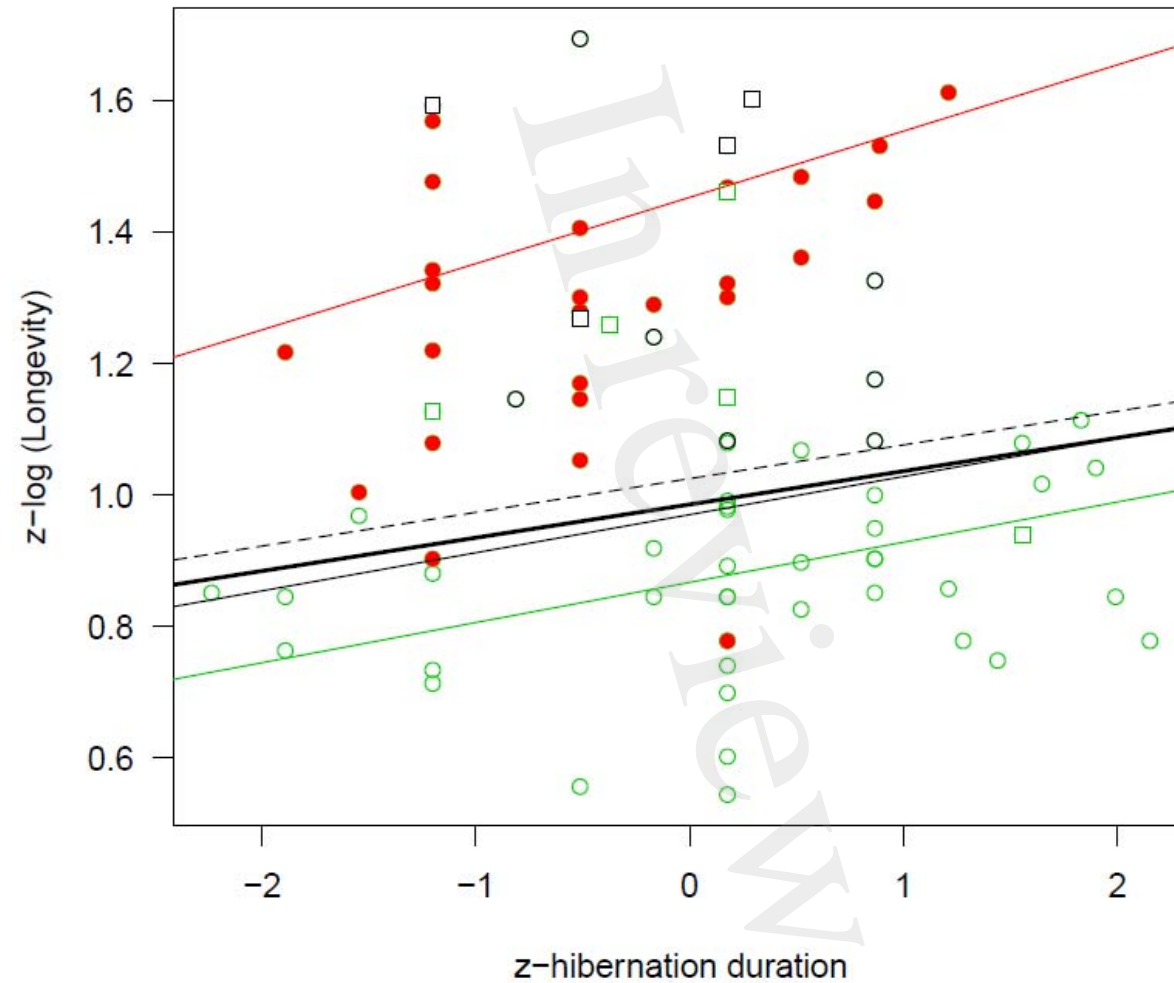
			λ_{ML}				$\lambda = 0$		
			λ_{ML}	$\beta \pm SE$	t	P	$\beta \pm SE$	t	P
Phylogenetic correction (PGLS)	Model 1: All hibernators (82 species)	Intercept	$\lambda_{ML} = 0.736$ $CI_{95} = [NA-0.924]$	0.986 ± 0.111	8.847	< 0.001***	0.834 ± 0.032	25.778	< 0.001***
		z-Hibernation duration		0.051 ± 0.020	2.484	0.015 *	0.028 ± 0.020	1.343	0.183
		z-log (Body mass)		0.163 ± 0.043	3.800	< 0.001***	0.216 ± 0.026	8.409	< 0.001***
		bat		0.531 ± 0.170	3.131	0.002**	0.656 ± 0.060	10.903	< 0.001***
	Model 2: Hibernators without bats (55 species)	Intercept	$\lambda_{ML} = 0.849$ $CI_{95} = [0.238-0.969]$	0.970 ± 0.112	8.682	< 0.001***	0.841 ± 0.031	27.439	< 0.001***
		z-Hibernation duration		0.058 ± 0.022	2.645	0.011 *	0.004 ± 0.022	0.200	0.842
		z-log (Body mass)		0.171 ± 0.038	4.442	< 0.001***	0.217 ± 0.024	8.920	< 0.001***
		arboreality		0.191 ± 0.070	2.738	0.008**	0.173 ± 0.051	3.409	0.001**
	Model 3: Deep hibernators without bats (46 species)	Intercept	$\lambda_{ML} = 0.850$ $CI_{95} = [0.480-0.960]$	1.025 ± 0.107	9.611	< 0.001***	0.876 ± 0.026	33.483	< 0.001***
		z-Hibernation duration		0.051 ± 0.022	2.279	0.028*	0.008 ± 0.023	0.342	0.734
	Model 4: Small hibernators (< 1.5 kg) without bats (44 species)	Intercept	$\lambda_{ML} = 0.740$ $CI_{95} = [0.293-0.924]$	0.867 ± 0.084	10.240	< 0.001***	0.820 ± 0.029	28.543	< 0.001***
		z-Hibernation duration		0.061 ± 0.020	2.994	0.005**	0.024 ± 0.021	1.148	0.258
z-log (Body mass)		0.014 ± 0.053		0.264	0.793	0.121 ± 0.042	2.864	0.007**	
arboreality		0.204 ± 0.069		2.937	0.005**	0.191 ± 0.048	4.002	< 0.001***	
No phylogenetic correction (linear model)	Model 5: Bats only (27 species)	Intercept	NA	1.453 ± 0.168	8.619	< 0.001*	NA		
		z-Hibernation duration		0.101 ± 0.045	2.215	0.036*			
		z-log (Body mass)		0.141 ± 0.179	0.785	0.440			

Table 2. Z-standardized model estimates (β) for the effects of hibernation season duration and body mass on species maximum longevity. The phylogenetic effect is estimated by λ_{ML} . Both body mass and longevity were log-transformed before the analyses. For comparison, we have provided estimates for λ constrained to zero (no effect of phylogeny). The model for bats was a simple linear model not controlling for phylogeny, due to limited sample size in this group. In the model with all hibernators, the NA value in the confidence interval for λ_{ML} indicates that the caper package could not calculate the full confidence interval. An NA value is considered as 0.



703

704 Figure 1. Effects of hibernation season duration and body mass on longevity. Z-standardized model coefficients are presented \pm 95% Confidence
 705 Interval ($1.96 \times SE$). Both body mass and longevity were log-transformed before the analyses. The effect sizes are presented for PGLS models for all
 706 mammals ($N = 82$), mammals without bats ($N = 55$), deep hibernators without bats ($n=46$) and small mammals without bats ($N = 44$). For
 707 comparison, effect sizes from a simple linear model not accounting for phylogeny are presented for bats only ($N = 27$).



708

709 Figure 2. Relationship between hibernation season duration (standardized) and longevity (log-transformed and standardized). The regression lines are
 710 presented for PGLS models for all mammals (bold black line, $N = 82$, $p=0.015$), all hibernators without bats (black line, $N = 55$, $p=0.011$), deep
 711 hibernators without bats (dashed line, $N = 46$, $p=0.028$) and small hibernators without bats (green line, $N = 44$, $p=0.005$). For comparison, effect sizes
 712 from a simple linear model not accounting for phylogeny are presented for bats only (red, $N = 27$, $p=0.036$). Full red circles highlight bat species, the

713 squares highlight species reducing their energy expenditure during hibernation by less than 90% compared to the euthermic state, green item highlight
714 species below 1.5kg, and black circle highlight all remaining hibernators above 1.5kg in the data set. Please note that some dots referring to bat species
715 are superimposed because the corresponding species have exact same hibernation season durations and longevities.

In review

<i>Species</i>	<i>Family</i>	<i>Exclusion criteria</i>	<i>Longevity data</i>	<i>Hibernation data</i>	<i>Species included in study</i>
<i>Echinops telfairi</i>	Afrosoricida	No	AnAge	No data	No
<i>Ursus americanus</i>	Carnivora	No	AnAge	Yes	Yes
<i>Ursus arctos</i>	Carnivora	No	AnAge	Yes	Yes
<i>Ursus maritimus</i>	Carnivora	Criteria 1			No
<i>Ursus thibetanus</i>	Carnivora	No	AnAge	Yes	Yes
<i>Antrozous pallidus</i>	Chiroptera	No	AnAge	No data	No
<i>Barbastella barbastellus</i>	Chiroptera	No	AnAge	Yes	Yes
<i>Corynorhinus rafinesquii</i>	Chiroptera	No	PanTHERIA	Yes	Yes
<i>Corynorhinus townsendii</i>	Chiroptera	No	PanTHERIA	No data	No
<i>Eptesicus fuscus</i>	Chiroptera	No	AnAge	Yes	Yes
<i>Eptesicus nilssonii</i>	Chiroptera	No	AnAge	Yes	Yes
<i>Eptesicus serotinus</i>	Chiroptera	No	AnAge	Yes	Yes
<i>Lasionycteris noctivagans</i>	Chiroptera	No	AnAge	No data	No
<i>Lasiurus cinereus</i>	Chiroptera	No	AnAge	Yes	Yes
<i>Miniopterus schreibersii</i>	Chiroptera	No	AnAge	Yes	Yes
<i>Myotis austroriparius</i>	Chiroptera	No	PanTHERIA	Yes	Yes
<i>Myotis bechsteinii</i>	Chiroptera	No	AnAge	No data	No
<i>Myotis blythii</i>	Chiroptera	No	AnAge	No data	No
<i>Myotis brandtii</i>	Chiroptera	No	AnAge	Yes	Yes
<i>Myotis californicus</i>	Chiroptera	No	PanTHERIA	No data	No
<i>Myotis dasycneme</i>	Chiroptera	No	PanTHERIA	Yes	Yes
<i>Myotis daubentonii</i>	Chiroptera	No	AnAge	Yes	Yes
<i>Myotis emarginatus</i>	Chiroptera	No	AnAge	No data	No
<i>Myotis evotis</i>	Chiroptera	No	AnAge	No data	No
<i>Myotis grisescens</i>	Chiroptera	No	AnAge	Yes	Yes
<i>Myotis keenii</i>	Chiroptera	No	AnAge	Yes	Yes
<i>Myotis leibii</i>	Chiroptera	No	AnAge	No data	No
<i>Myotis lucifugus</i>	Chiroptera	No	AnAge	Yes	Yes
<i>Myotis myotis</i>	Chiroptera	No	AnAge	Yes	Yes
<i>Myotis mystacinus</i>	Chiroptera	No	AnAge	No data	No
<i>Myotis nattereri</i>	Chiroptera	No	AnAge	No data	No
<i>Myotis sodalis</i>	Chiroptera	No	AnAge	Yes	Yes
<i>Myotis thysanodes</i>	Chiroptera	No	AnAge	No data	No
<i>Myotis velifer</i>	Chiroptera	No	AnAge	Yes	Yes
<i>Myotis volans</i>	Chiroptera	No	AnAge	No data	No
<i>Myotis yumanensis</i>	Chiroptera	No	AnAge	No data	No
<i>Nyctalus leisleri</i>	Chiroptera	No	No data		No
<i>Nyctalus noctula</i>	Chiroptera	No	AnAge	Yes	Yes
<i>Pipistrellus hesperus</i>	Chiroptera	No	PanTHERIA	No data	No
<i>Pipistrellus nathusii</i>	Chiroptera	No	AnAge	No data	No
<i>Pipistrellus pipistrellus</i>	Chiroptera	No	AnAge	Yes	Yes
<i>Pipistrellus subflavus</i>	Chiroptera	No	AnAge	Yes	Yes
<i>Plecotus auritus</i>	Chiroptera	No	AnAge	Yes	Yes
<i>Plecotus austriacus</i>	Chiroptera	No	AnAge	Yes	Yes
<i>Rhinolophus ferrumequinum</i>	Chiroptera	No	AnAge	Yes	Yes

<i>Rhinolophus hipposideros</i>	Chiroptera	No	AnAge	Yes	Yes
<i>Rhinolophus megaphyllus</i>	Chiroptera	No	No data		No
<i>Vespertilio murinus</i>	Chiroptera	No	AnAge	No data	No
<i>Zaedyus pichiy</i>	Cingulata	No	AnAge	yes	No*
<i>Acrobates pygmaeus</i>	Diprotodontia	Criteria 3			No
<i>Burramys parvus</i>	Diprotodontia	No	AnAge	Yes	Yes
<i>Cercartetus nanus</i>	Diprotodontia	Criteria 3			No
<i>Erinaceus concolor</i>	Erinaceomorpha	No	AnAge	Yes	Yes
<i>Erinaceus europaeus</i>	Erinaceomorpha	No	AnAge	Yes	Yes
<i>Hemiechinus auritus</i>	Erinaceomorpha	No	AnAge	Yes	Yes
<i>Paraechinus hypomelas</i>	Erinaceomorpha	No	AnAge	No data	No
<i>Dromiciops gliroides</i>	Microbiotheria	No	No data		No
<i>Tachyglossus aculeatus</i>	Monotremata	No	AnAge	Yes	Yes
<i>Cheirogaleus major</i>	Primates	No	AnAge	Yes	Yes
<i>Cheirogaleus medius</i>	Primates	No	AnAge	Yes	Yes
<i>Microcebus murinus</i>	Primates	No	AnAge	Yes	Yes
<i>Microcebus rufus</i>	Primates	No			No
<i>Allactaga euphratica</i>	Rodentia	No	AnAge	No data	No
<i>Callospermophilus lateralis</i>	Rodentia	No	AnAge	Yes	Yes
<i>Callospermophilus saturatus</i>	Rodentia	No	No data		No
<i>Chaetodipus formosus</i>	Rodentia	No	AnAge	Yes	Yes
<i>Cricetus cricetus</i>	Rodentia	No	AnAge	Yes	Yes
<i>Cynomys gunnisoni</i>	Rodentia	No	No data		No
<i>Cynomys ludovicianus</i>	Rodentia	Criteria 1			No
<i>Eliomys quercinus</i>	Rodentia	No	AnAge	Yes	Yes
<i>Glis glis</i>	Rodentia	No	Other source	Yes	Yes
<i>Graphiurus murinus</i>	Rodentia	No	AnAge	No data	No
<i>Jaculus jaculus</i>	Rodentia	No	AnAge	No data	No
<i>Marmota bobak</i>	Rodentia	No	PanTHERIA	Yes	Yes
<i>Marmota flaviventris</i>	Rodentia	No	AnAge	Yes	Yes
<i>Marmota marmota</i>	Rodentia	No	AnAge	Yes	Yes
<i>Marmota monax</i>	Rodentia	No	AnAge	Yes	Yes
<i>Marmota vancouverensis</i>	Rodentia	No	AnAge	Yes	Yes
<i>Mesocricetus auratus</i>	Rodentia	No	AnAge	No data	No
<i>Microdipodops megacephalus</i>	Rodentia	No	Other source	Yes	Yes
<i>Muscardinus avellanarius</i>	Rodentia	No	Other source	Yes	Yes
<i>Napaeozapus insignis</i>	Rodentia	No	PanTHERIA	Yes	Yes
<i>Otospermophilus beecheyi</i>	Rodentia	No	Other source	Yes	Yes
<i>Perognathus flavescens</i>	Rodentia	No	No data		No
<i>Perognathus flavus</i>	Rodentia	No	PanTHERIA	No data	No
<i>Perognathus longimembris</i>	Rodentia	No	AnAge	Yes	Yes
<i>Perognathus parvus</i>	Rodentia	No	AnAge	Yes	Yes
<i>Sicista betulina</i>	Rodentia	No	Other source	Yes	Yes
<i>Spermophilus citellus</i>	Rodentia	No	AnAge	Yes	Yes
<i>Spermophilus dauricus</i>	Rodentia	No	Other source	Yes	Yes

<i>Tamias amoenus</i>	Rodentia	No	Other source	Yes	Yes
<i>Tamias minimus</i>	Rodentia	No	AnAge	No data	No
<i>Tamias sibiricus</i>	Rodentia	No	AnAge	Yes	Yes
<i>Tamias striatus</i>	Rodentia	No	AnAge	Yes	Yes
<i>Tamias townsendii</i>	Rodentia	No	AnAge	Yes	Yes
<i>Urocitellus armatus</i>	Rodentia	No	Other source	Yes	Yes
<i>Urocitellus beldingi</i>	Rodentia	No	Other source	Yes	Yes
<i>Urocitellus columbianus</i>	Rodentia	No	Other source	Yes	Yes
<i>Urocitellus parryii</i>	Rodentia	No	Other source	Yes	Yes
<i>Urocitellus richardsonii</i>	Rodentia	No	Other source	Yes	Yes
<i>Urocitellus townsendii</i>	Rodentia	No	No data		No
<i>Zapus hudsonius</i>	Rodentia	No	AnAge	Yes	Yes
<i>Zapus princeps</i>	Rodentia	No	Other source	Yes	Yes
<i>Amblysomus hottentotus</i>	Afrosoricida	No	No data		No
<i>Setifer setosus</i>	Afrosoricida	No	AnAge	Yes	Yes
<i>Tenrec ecaudatus</i>	Afrosoricida	No	AnAge	Yes	Yes
<i>Meles meles</i>	Carnivora	No	AnAge	Yes	Yes
<i>Chalinolobus gouldii</i>	Chiroptera	No	No data		No
<i>Hipposideros terasensis</i>	Chiroptera	No	No data		No
<i>Lasiurus borealis</i>	Chiroptera	No	No data		No
<i>Mops condylurus</i>	Chiroptera	No	No data		No
<i>Myotis adversus</i>	Chiroptera	No	No data		No
<i>Nyctophilus bifax</i>	Chiroptera	No	No data		No
<i>Nyctophilus geoffroyi</i>	Chiroptera	No	No data		No
<i>Nyctophilus gouldi</i>	Chiroptera	No	No data		No
<i>Rhinopoma microphyllum</i>	Chiroptera	No	No data		No
<i>Tadarida aegyptiaca</i>	Chiroptera	No	No data		No
<i>Tadarida brasiliensis</i>	Chiroptera	No	AnAge	No data	No
<i>Tadarida teniotis</i>	Chiroptera	No	AnAge	No data	No
<i>Vespadelus vulturnus</i>	Chiroptera	No	No data		No
<i>Cercartetus concinnus</i>	Diprotodontia	Criteria 3			No
<i>Cercartetus lepidus</i>	Diprotodontia	Criteria 3			No
<i>Atelerix algirus</i>	Eulipotyphla	No	PanTHERIA	Yes	Yes
<i>Atelerix frontalis</i>	Eulipotyphla	No	No data		No
<i>Elephantulus edwardii</i>	Macroscelidea	Criteria 3			No
<i>Elephantulus myurus</i>	Macroscelidea	Criteria 3			No
<i>Cheirogaleus crossleyi</i>	Primates	No	No data		No
<i>Microcebus griseorufus</i>	Primates	No	No data		No
<i>Allactaga williamsi</i>	Rodentia	No	No data		No
<i>Cynomys parvidens</i>	Rodentia	No	No data		No
<i>Cynomys leucurus</i>	Rodentia	No	No data		No
<i>Glirulus japonicus</i>	Rodentia	No	AnAge	Yes	Yes
<i>Graphiurus ocellaris</i>	Rodentia	No	No data		No
<i>Ictidomys tridecemlineatus</i>	Rodentia	No	AnAge	Yes	Yes
<i>Ictidomys mexicanus</i>	Rodentia	No	No data		No

<i>Jaculus orientalis</i>	Rodentia	No	AnAge	No data	No
<i>Marmota broweri</i>	Rodentia	No	No data		No
<i>Mesocricetus brandti</i>	Rodentia	No	AnAge	No data	No
<i>Microdipodops pallidus</i>	Rodentia	No	No data		No
<i>Otospermophilus variegatus</i>	Rodentia	No	AnAge	Yes	Yes
<i>Spermophilus xanthopymnus</i>	Rodentia	No	No data		No
<i>Urocitellus elegans</i>	Rodentia	No	No data		No
<i>Xerospermophilus tereticaudus</i>	Rodentia	No	AnAge	Yes	Yes
<i>Myotis septentrionalis</i>	Chiroptera	No	Other source	Yes	Yes
<i>Myotis kuhlii</i>	Chiroptera	No	AnAge	Yes	Yes
<i>Rhinolophus euryale</i>	Chiroptera	No	Other source	Yes	Yes
<i>Dryomys nitedula</i>	Rodentia	No	Other source	Yes	Yes
<i>Marmota caligata</i>	Rodentia	No	AnAge	Yes	Yes
<i>Poliocitellus franklinii</i>	Rodentia	No	AnAge	Yes	Yes
<i>Spermophilus pygmaeus</i>	Rodentia	No	AnAge	Yes	Yes
<i>Urocitellus brunneus</i>	Rodentia	No	Other source	Yes	Yes
<i>Xerospermophilus mohavensis</i>	Rodentia	No	AnAge	Yes	Yes

716

717

718 Table S1: Summary of the hibernators selected in this study among the 152 listed hibernators.
719 Species (1) in black are listed in Turbill et al (2011), (2) in dark blue represent the other species
720 listed by Ruf and Geiser (2015) and (3) in light blue represent other known hibernators. AnAge
721 refers to AnAge data base (The Animal Aging and Longevity Database;
722 https://genomics.senescence.info/species/search_list.php; Human Ageing and Genomic Resources;
723 Magalhães and Costa, 2009), and PanTHERIA refers to the PanTHERIA data base
724 (<https://ecologicaldata.org/wiki/PanTHERIA>; Ecological Archives, Ecological Society of America;
725 Jones et al., 2009). We mention the new nomenclature for ground squirrel species, which may not
726 correspond to the nomenclature of the lists presented. Some species were first excluded according
727 to the exclusion criteria listed in the publication. We then investigate the longevity of hibernators
728 according to the methods described in the publication. Only species for which we have found both
729 the hibernation season duration and longevity were included in the study. All references for
730 longevity and hibernation duration data are presented in Table S2.

731 *Note that longevity (12.5 years) and hibernation season duration (90 day) of *Zaedyus pichiy* are
732 known (Magalhaes and Costa, 2009; Superina and Abba, 2014) but by including this species the
733 binary condition of the phylogenetic tree was not satisfied. A rooted tree is considered binary if all
734 nodes (including the root node) have exactly two descendant nodes. This condition was tested using
735 the ‘ape 5.0’ packages in R v. 3.6.2.

736 De Magalhaes, J. P., & Costa, J. (2009). A database of vertebrate longevity records and their
737 relation to other life-history traits. *Journal of evolutionary biology*, 22(8), 1770-1774.

738 Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., ... & Connolly, C.
739 (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and
740 recently extinct mammals: *Ecological Archives* E090-184. *Ecology*, 90(9), 2648-2648.

- 741 Ruf, T., & Geiser, F. (2015). Daily torpor and hibernation in birds and mammals. *Biological*
742 *Reviews*, 90(3), 891-926.
- 743 Superina, M., & Abba, A. M. (2014). *Zaedyus pichiy* (Cingulata: Dasypodidae). *Mammalian*
744 *Species*, 46(905), 1-10.
- 745 Turbill, C., Bieber, C., & Ruf, T. (2011). Hibernation is associated with increased survival and the
746 evolution of slow life histories among mammals. *Proceedings of the Royal Society B: Biological*
747 *Sciences*, 278(1723), 3355-3363.
- 748
- 749
- 750

In review

<i>Species</i>	<i>Family</i>	<i>Hibernation season duration (day)</i>	<i>Body mass (g)</i>	<i>Longevity (year)</i>	<i>Arboreality</i>	<i>Wild or Captivity</i>
<i>Burramys parvus</i>	Burramyidae	210 ^{1,2}	45 ³	12 ³	Yes ⁴	Wild
<i>Cheirogaleus major</i>	Cheirogaleidae	150 ⁵⁻⁷	395 ³	13.4 ³	Yes ^{8,9}	Captivity
<i>Cheirogaleus medius</i>	Cheirogaleidae	210 ¹⁰	380 ³	29 ³	Yes ^{4,8,11}	Captivity
<i>Microcebus murinus</i>	Cheirogaleidae	186 ¹²	64.8 ³	18.2 ³	Yes ^{4,13}	Captivity
<i>Cricetus cricetus</i>	Cricetidae	180 ¹⁴	506.7 ³	3.6 ³	No ¹⁵	Captivity
<i>Napaeozapus insignis</i>	Dipodidae	210 ^{16*}	22.25 ¹⁷	4 ¹⁷	No ¹⁸	Wild
<i>Sicista betulina</i>	Dipodidae	210 ^{19*}	8.92 ¹⁷	3.5 ²⁰	No ⁹	Wild
<i>Zapus hudsonius</i>	Dipodidae	265 ²¹	18 ³	5.6 ³	No ²²	Captivity
<i>Zapus princeps</i>	Dipodidae	296 ²³	27.2 ¹⁷	6 ²⁴	No ²⁵	Wild
<i>Atelerix algirus</i>	Erinaceidae	120 ²⁶	958 ¹⁷	7 ¹⁷	No ²⁷	Captivity
<i>Erinaceus concolor</i>	Erinaceidae	210 ²⁸	719 ³	7 ³	No ⁹	Captivity
<i>Erinaceus europaeus</i>	Erinaceidae	225 ²⁹	750 ³	11.7 ³	No ⁴	Captivity
<i>Hemiechinus auritus</i>	Erinaceidae	150 ³⁰	342 ³	7.6 ³	No ⁹	Captivity
<i>Dryomys nitedula</i>	Gliridae	240 ³¹	26 ³	8 ³¹	Yes ^{9,32}	Wild
<i>Eliomys quercinus</i>	Gliridae	210 ³³	82.5 ³	5.5 ³	Yes ^{9,34}	Captivity
<i>Glirulus japonicus</i>	Gliridae	195 ³⁵	27 ³	7 ³	Yes ^{9,36}	Captivity
<i>Glis glis</i>	Gliridae	282 ³⁷	125 ³	13 ³⁸	Yes ^{9,39}	Wild
<i>Muscardinus avellanarius</i>	Gliridae	210 ⁴⁰	27.3 ³	6 ^{40,41}	Yes ^{9,42}	Wild
<i>Chaetodipus formosus</i>	Heteromyidae	105 ⁴³	19 ³	7.1 ³	No ⁹	Captivity
<i>Microdipodops megacephalus</i>	Heteromyidae	150 ⁴⁴	12.3 ¹⁷	5.42 ¹⁷	No ⁴⁵	Captivity
<i>Perognathus longimembris</i>	Heteromyidae	195 ⁴³	8 ³	8.3 ³	No ⁹	Captivity
<i>Perognathus parvus</i>	Heteromyidae	120 ⁴⁶	20.1 ³	5.8 ³	No ⁴⁷	Captivity
<i>Miniopterus schreibersii</i>	Miniopteridae	150 ^{48*}	13 ³	22 ³	No ⁴	Wild
<i>Meles meles</i>	Mustelidae	180 ^{49*}	13000 ³	18.6 ³	No ⁴	Captivity
<i>Rhinolophus euryale</i>	Rhinolophidae	150 ⁵⁰⁻⁵²	8.2 ³	21 ⁵³	No ⁹	Wild

<i>Rhinolophus ferrumequinum</i>	Rhinolophidae	225 ⁵⁴	22.875 ³	30.5 ³	No ⁴	Wild
<i>Rhinolophus hipposideros</i>	Rhinolophidae	210 ⁵⁵	4.6 ³	29.4 ³	No ⁴	Wild
<i>Callospermophilus lateralis</i>	Sciuridae	274 ⁵⁶	157.6 ³	10.4 ³	No ⁵⁷	Captivity
<i>Ictidomys tridecemlineatus</i>	Sciuridae	225 ⁵⁸	172.7 ³	7.9 ³	No ⁵⁹	Captivity
<i>Marmota bobak</i>	Sciuridae	240 ^{60*}	7300 ¹⁷	15 ¹⁷	No ⁹	Wild
<i>Marmota caligata</i>	Sciuridae	240 ^{61*}	4300 ³	12.1 ³	No ⁶¹	Captivity
<i>Marmota flaviventris</i>	Sciuridae	240 ⁶²	3500 ³	21.2 ³	No ⁶³	Captivity
<i>Marmota marmota</i>	Sciuridae	195 ⁶⁴	3500 ³	17.4 ³	No ⁴	Captivity
<i>Marmota monax</i>	Sciuridae	166.9 ⁶⁵	4000 ³	14 ³	No ⁴	Captivity
<i>Marmota vancouverensis</i>	Sciuridae	210 ⁶⁶	4750 ³	12.1 ³	No ⁴	Captivity
<i>Otospermophilus beecheyi</i>	Sciuridae	210 ⁶⁷	508.5 ⁶⁸	5 ⁵³	No ⁶⁹	Wild
<i>Otospermophilus variegatus</i>	Sciuridae	210 ^{70*}	663 ³	9.8 ³	Yes ⁷¹⁻⁷⁴	Captivity
<i>Poliocitellus franklinii</i>	Sciuridae	255 ⁷⁵	459 ³	7.2 ³	No ⁷⁶	Captivity
<i>Spermophilus citellus</i>	Sciuridae	225 ⁷⁷	217 ³	6.7 ³	No ⁴	Captivity
<i>Spermophilus dauricus</i>	Sciuridae	210 ^{78*}	223.8 ⁶⁸	7 ⁷⁸	No ⁹	Wild
<i>Spermophilus pygmaeus</i>	Sciuridae	240 ⁷⁹	136 ³	7.1 ³	No ⁹	Captivity
<i>Tamias amoenus</i>	Sciuridae	150 ⁸⁰	50.63 ¹⁷	5.17 ⁸¹	Yes ^{9,82-84}	Wild
<i>Tamias sibiricus</i>	Sciuridae	210 ⁸⁵	85 ³	9.6 ³	Yes ^{9,84-86}	Captivity
<i>Tamias striatus</i>	Sciuridae	210 ⁸⁷	96 ³	9.5 ³	Yes ^{9,84,88-90}	Captivity
<i>Tamias townsendii</i>	Sciuridae	135 ⁹¹	75 ³	9.3 ³	Yes ^{9,84,92-94}	Captivity
<i>Urocitellus armatus</i>	Sciuridae	289 ⁹⁵	306.48 ¹⁷	7 ⁹⁶	No ⁹⁷	Wild
<i>Urocitellus beldingi</i>	Sciuridae	270 ⁹⁸	265.2 ⁶⁸	12 ⁹⁹	No ¹⁰⁰	Wild
<i>Urocitellus brunneus</i>	Sciuridae	240 ¹⁰¹	300 ¹⁷	8 ¹⁰¹	No ¹⁰²	Wild
<i>Urocitellus columbianus</i>	Sciuridae	285 ¹⁰³	470.94 ¹⁷	11 ¹⁰⁴	No ¹⁰⁵	Wild
<i>Urocitellus parryii</i>	Sciuridae	240 ¹⁰⁶	524.3 ⁶⁸	10 ¹⁰⁷	No ¹⁰⁸	Wild
<i>Urocitellus richardsonii</i>	Sciuridae	258 ¹⁰⁹	325.1 ¹⁷	6 ¹¹⁰	No ¹¹¹	Wild
<i>Xerospermophilus mohavensis</i>	Sciuridae	210 ^{112*}	150 ³	7.8 ³	No ¹¹³	Captivity

<i>Xerospermophilus tereticaudus</i>	Sciuridae	240 ¹¹⁴	163.3 ³	8.9 ³	No ¹¹²	Captivity
<i>Tachyglossus aculeatus</i>	Tachyglossidae	180 ¹¹⁵	3500 ³	49.5 ³	No ⁴	Captivity
<i>Setifer setosus</i>	Tenrecidae	210 ¹¹⁶	225 ³	14.1 ³	Yes ^{4,117,118}	Captivity
<i>Tenrec ecaudatus</i>	Tenrecidae	270 ¹¹⁹	900 ³	8.7 ³	No ¹²⁰	Captivity
<i>Ursus americanus</i>	Ursidae	210 ^{121*}	154250 ³	34 ³	No ⁴	Captivity
<i>Ursus arctos</i>	Ursidae	215 ¹²²	277500 ³	40 ³	No ⁴	Captivity
<i>Ursus thibetanus</i>	Ursidae	150 ¹²³	103750 ³	39.2 ³	Yes ^{4,124,125}	Captivity
<i>Barbastella barbastellus</i>	Vespertilionidae	225 ¹²⁶	10.25 ³	23 ³	No ⁴	Wild
<i>Corynorhinus rafinesquii</i>	Vespertilionidae	135 ¹²⁷	9.15 ¹⁷	10.1 ¹⁷	No ¹²⁸	Wild
<i>Eptesicus fuscus</i>	Vespertilionidae	180 ¹²⁹	23 ³	19 ³	No ⁴	Wild
<i>Eptesicus nilssonii</i>	Vespertilionidae	180 ^{130*}	13 ³	20 ³	No ⁴	Wild
<i>Eptesicus serotinus</i>	Vespertilionidae	210 ¹³¹	18.2 ³	21 ³	No ⁴	Wild
<i>Lasiurus cinereus</i>	Vespertilionidae	180 ¹³²	24 ³	14 ³	No ⁴	Wild
<i>Myotis austroriparius</i>	Vespertilionidae	210 ^{133,134*}	7.35 ¹⁷	6 ¹⁷	No ¹³³	Wild
<i>Myotis brandtii</i>	Vespertilionidae	255 ^{135*}	7 ³	41 ³	No ⁴	Wild
<i>Myotis dasycneme</i>	Vespertilionidae	195 ^{136*}	15.16 ¹⁷	19.5 ¹⁷	No ⁴	Wild
<i>Myotis daubentonii</i>	Vespertilionidae	240 ¹³⁷	8.5 ³	28 ³	No ⁴	Wild
<i>Myotis grisescens</i>	Vespertilionidae	120 ^{138*}	9.25 ³	16.5 ³	No ⁴	Wild
<i>Myotis keenii</i>	Vespertilionidae	180 ¹³⁹	7.4 ³	19 ³	No ⁴	Wild
<i>Myotis lucifugus</i>	Vespertilionidae	241 ¹⁴⁰	10 ³	34 ³	No ⁴	Wild
<i>Myotis myotis</i>	Vespertilionidae	150 ¹⁴¹	28.55 ³	37.1 ³	No ⁴	Wild
<i>Myotis septentrionalis</i>	Vespertilionidae	180 ¹⁴²	7 ¹⁴³	19 ¹⁴⁴	No ¹⁴⁵	Wild
<i>Myotis sodalis</i>	Vespertilionidae	210 ¹⁴⁶	7.7 ³	20 ³	No ⁴	Wild
<i>Myotis velifer</i>	Vespertilionidae	180 ¹⁴⁷	10.1 ³	11.3 ³	No ⁴	Wild
<i>Nyctalus noctula</i>	Vespertilionidae	150 ^{52,148}	27.75 ³	12 ³	No ⁴	Wild
<i>Pipistrellus kuhlii</i>	Vespertilionidae	150 ^{149*}	6 ³	8 ³	No ⁴	Wild
<i>Pipistrellus pipistrellus</i>	Vespertilionidae	150 ^{52,150}	5 ³	16.6 ³	No ⁴	Wild

<i>Pipistrellus subflavus</i>	Vespertilionidae	180 ¹⁵¹	7.5 ³	14.8 ³	No ⁴	Wild
<i>Plecotus auritus</i>	Vespertilionidae	150 ¹⁵²	7.8 ³	30 ³	No ⁴	Wild
<i>Plecotus austriacus</i>	Vespertilionidae	180 ¹⁵²	12 ³	25.5 ³	No ⁴	Wild

751

752 Table S2: Data on hibernation season duration, body mass, longevity and arboreality lifestyle of all mammals studied in the different models.
 753 Hibernation season duration with (*) corresponds to publications for which the methodology used to determine this duration could not be verified.
 754 The “Wild or Captivity” parameter refers to the source of longevity data. The “arboreality” parameter distinguishes between species considered
 755 arboreal and semi-arboreal (Yes) and non-arboreal (No). Brown bear (*Ursus arctos*) and American black bear (*Ursus americanus*) have been defined
 756 as non-arboreal, as in Healy et al, 2014, as the majority of adults are losing this lifestyle¹⁵³ contrary to Asian black bear (*Ursus thibetanus*)¹²⁴. Bats
 757 were considered to be non-arboreal even though it nests in trees as nesting in a protected area is a common characteristic of all bats and therefore
 758 already taken into account in the “bat (yes/no)” factor.

759

- 760 1. Körtner, G. & Geiser, F. Ecology of natural hibernation in the marsupial mountain pygmy-possum (*Burramys parvus*). *Oecologia* **113**, 170–
 761 178 (1998).
- 762 2. Körtner, G., Song, X. & Geiser, F. Rhythmicity of torpor in a marsupial hibernator, the mountain pygmy-possum (*Burramysparvus*), under
 763 natural and laboratory conditions. *Journal of comparative Physiology B* **168**, 631–638 (1998).
- 764 3. Magalhães, J. P. D. & Costa, J. A database of vertebrate longevity records and their relation to other life-history traits. *Journal of*
 765 *Evolutionary Biology* **22**, 1770–1774 (2009).
- 766 4. Healy, K. *et al.* Ecology and mode-of-life explain lifespan variation in birds and mammals. *Proceedings of the Royal Society B: Biological*
 767 *Sciences* **281**, 20140298 (2014).
- 768 5. Wright, P. C. & Martin, L. B. Predation, Pollination and Torpor in Two Nocturnal Prosimians: *Cheirogaleus Major* and *Microcebus Rufus* in
 769 the Rain Forest of Madagascar. in *Creatures of the Dark: The Nocturnal Prosimians* (eds. Alterman, L., Doyle, G. A. & Izard, M. K.) 45–60
 770 (Springer US, 1995). doi:10.1007/978-1-4757-2405-9_4.
- 771 6. Lahann, P. Biology of *Cheirogaleus major* in a Littoral Rain Forest in Southeast Madagascar. *Int J Primatol* **28**, 895–905 (2007).

- 772 7. Schülke, O. & Ostner, J. Physiological ecology of cheirogaleid primates: variation in hibernation and torpor. *Acta Ethologica* **10**, 13–21
773 (2007).
- 774 8. Clutton-Brock, T. H. & Harvey, P. H. Primates, brains and ecology. *Journal of Zoology* **190**, 309–323 (1980).
- 775 9. Hidasi-Neto, J., Loyola, R. & Cianciaruso, M. V. Global and local evolutionary and ecological distinctiveness of terrestrial mammals:
776 identifying priorities across scales. *Diversity and Distributions* **21**, 548–559 (2015).
- 777 10. Dausmann, K. H., Glos, J., Ganzhorn, J. U. & Heldmaier, G. Hibernation in a tropical primate. *Nature* **429**, 825–826 (2004).
- 778 11. Lemelin, P. & Schmitt, D. Seasonal variation in body mass and locomotor kinetics of the fat-tailed dwarf lemur (*Cheirogaleus medius*).
779 *Journal of Morphology* **260**, 65–71 (2004).
- 780 12. Schmid, J. & Kappeler, P. M. Fluctuating sexual dimorphism and differential hibernation by sex in a primate, the gray mouse lemur
781 (*Microcebus murinus*). *Behavioral Ecology and Sociobiology* **43**, 125–132 (1998).
- 782 13. Toussaint, S. *et al.* Food acquisition on arboreal substrates by the grey mouse lemur: implication for primate grasping evolution. *Journal of*
783 *Zoology* **291**, 235–242 (2013).
- 784 14. Siutz, C., Franceschini, C. & Millesi, E. Sex and age differences in hibernation patterns of common hamsters: adult females hibernate for
785 shorter periods than males. *Journal of Comparative Physiology B* **186**, 801–811 (2016).
- 786 15. Kryštufek, B., Hoffmann, I. E., Nedyalkov, N., Pozdnyakov, A. & Vohralík, V. *Cricetus cricetus* (Rodentia: Cricetidae). *Mamm Species* **52**,
787 10–26 (2020).
- 788 16. Wrigley, R. E. *Systematics and biology of the woodland jumping mouse, Napaeozapus insignis* 47. (Urbana, University of Illinois Press,
789 1972).
- 790 17. Jones, K. E. *et al.* PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals.
791 *Ecology* **90**, 2648–2648 (2009).
- 792 18. Whitaker, J. O. & Wrigley, R. E. *Napaeozapus insignis*. *Mamm Species* 1–6 (1972) doi:10.2307/3503916.
- 793 19. Johansen, K. & Krog, J. Diurnal body temperature variations and hibernation in the birchmouse, *Sicista betulina*. *American Journal of*
794 *Physiology-Legacy Content* **196**, 1200–1204 (1959).

- 795 20. Carey, J. R. & Judge, D. S. *Life Spans of Mammals, Birds, Amphibians, Reptiles, and Fish*. vol. 8 (2000).
- 796 21. Hoyle, J. & Boonstra, R. Life history traits of the meadow jumping mouse, *Zapus hudsonius*, in Southern Ontario. (1986).
- 797 22. Whitaker, J. O. *Zapus hudsonius*. *Mamm Species* 1–7 (1972) doi:10.2307/3504066.
- 798 23. Cranford, J. A. Hibernation in the Western Jumping Mouse (*Zapus princeps*). *J Mammal* **59**, 496–509 (1978).
- 799 24. Falk, J. W. & Millar, J. S. Reproduction by female *Zapus princeps* in relation to age, size, and body fat. *Can. J. Zool.* **65**, 568–571 (1987).
- 800 25. Hart, E. B., Belk, M. C., Jordan, E. & Gonzalez, M. W. *Zapus princeps*. *Mamm Species* 1–7 (2004) doi:10.1644/749.
- 801 26. Mouhoub sayah, C. *et al.* Road mortality of the Algerian hedgehog (*Atelerix algirus*) in the Soummam Valley (Algeria). *Revue d'écologie*
802 (2009).
- 803 27. Nowak, R. M. & Walker, E. P. *Walker's Mammals of the World*. (JHU Press, 1999).
- 804 28. Ahmet, Ö. Some biological, ecological and behavioural features of *Erinaceus concolor* Martin, 1838 (Mammalia: Insectivora) in Turkey.
805 *Gazi University Journal of Science* **19**, 91–97 (2006).
- 806 29. Rautio, A., Valtonen, A., Auttila, M. & Kunnasranta, M. Nesting patterns of European hedgehogs (*Erinaceus europaeus*) under northern
807 conditions. *Acta theriologica* **59**, 173–181 (2014).
- 808 30. SCHOENFELD, M. & Yoram, Y.-T. The biology of two species of hedgehogs, *Erinaceus europaeus concolor* and *Hemiechinus auritus*
809 *aegyptius*, in Israel. *Mammalia* **49**, 339–356 (1985).
- 810 31. Juškaitis, R. Ecology of the forest dormouse *Dryomys nitedula* (Pallas 1778) on the north-western edge of its distributional range. *Mammalia*
811 **79**, 33–41 (2015).
- 812 32. Juškaitis, R., Balčiauskas, L. & Šiožinytė, V. Nest site preference of forest dormouse *Dryomys nitedula* (Pallas) in the north-western corner
813 of the distribution range. *Pol. J. Ecol* **60**, 815–826 (2012).
- 814 33. Bertolino, S., Viano, C. & Currado, I. Population dynamics, breeding patterns and spatial use of the garden dormouse (*Eliomys quercinus*) in
815 an Alpine habitat. *Journal of Zoology* **253**, 513–521 (2001).

- 816 34. Bertolino, S. & Montezemolo, N. C. di. Garden dormouse (*Eliomys quercinus*) nest site selection in an alpine habitat. *Ethology Ecology & Evolution* **19**, 51–60 (2007).
- 818 35. Nakamura-Kojo, Y., Kojo, N., Ootsuka, T., Minami, M. & Tamate, H. B. Influence of tree resources on nest box use by the Japanese dormouse *Glirulus japonicus*. *Mammal study* **39**, 17–26 (2014).
- 820 36. Minato, S. & Doei, H. Arboreal activity of *Glirulus japonicus* (Rodentia: Myoxidae) confirmed by use of bryophytes as nest materials. *Acta Theriologica* **40**, 309–314 (1995).
- 822 37. Hoelzl, F. *et al.* How to spend the summer? Free-living dormice (*Glis glis*) can hibernate for 11 months in non-reproductive years. *J Comp Physiol B* **185**, 931–939 (2015).
- 824 38. Trout, R. C., Brooks, S. & Morris, P. Nest box usage by old edible dormice (*Glis glis*) in breeding and non-breeding years. *fozo* **64**, 320–324 (2015).
- 826 39. Kryštufek, B. *Glis glis* (Rodentia: Gliridae). *Mamm Species* **42**, 195–206 (2010).
- 827 40. Juškaitis, R. Life tables for the common dormouse *Muscardinus avellanarius* in Lithuania. *Acta Theriologica* **44**, 465–470 (1999).
- 828 41. Juškaitis, R. Summer mortality in the hazel dormouse (*Muscardinus avellanarius*) and its effect on population dynamics. *Acta Theriol* **59**, 311–316 (2014).
- 830 42. Bright, P. W. Behaviour of specialist species in habitat corridors: arboreal dormice avoid corridor gaps. *Animal Behaviour* **56**, 1485–1490 (1998).
- 832 43. Kenagy, G. J. & Bartholomew, G. A. Seasonal Reproductive Patterns in Five Coexisting California Desert Rodent Species: Ecological Archives M055-002. *Ecological Monographs* **55**, 371–397 (1985).
- 834 44. O’Farrell, M. J. Seasonal activity patterns of rodents in a sagebrush community. *Journal of Mammalogy* **55**, 809–823 (1974).
- 835 45. O’Farrell, M. J. & Blaustein, A. R. *Microdipodops megacephalus*. *Mamm Species* **46**, 1–3 (1974).
- 836 46. O’Farrell, T. P., Olson, R. J., Gilbert, R. O. & Hedlund, J. D. A Population of Great Basin Pocket Mice, *Perognathus parvus*, in the Shrub-Steppe of South-Central Washington. *Ecological Monographs* **45**, 1–28 (1975).
- 837

- 838 47. Verts, B. J. & Kirkland, G. L. *Perognathus parvus*. *Mamm Species* 1–8 (1988) doi:10.2307/3504324.
- 839 48. Oxberry, B. A. Female reproductive patterns in hibernating bats. *Reproduction* **56**, 359–367 (1979).
- 840 49. Kowalczyk, R., Jędrzejewska, B. & Zalewski, A. Annual and circadian activity patterns of badgers (*Meles meles*) in Białowieża Primeval
841 Forest (eastern Poland) compared with other Palaearctic populations. *Journal of Biogeography* **30**, 463–472 (2003).
- 842 50. Malinčiová, L., Hrehová, L., Maxinová, E., Uhrin, M. & Pristaš, P. The dynamics of Mediterranean horseshoe bat (*Rhinolophus euryale*,
843 Chiroptera) gut microflora during hibernation. <https://www.ingentaconnect.com/content/miiz/actac/2017/00000019/00000001/art00017> (2017)
844 doi:info:doi/10.3161/15081109ACC2017.19.1.017.
- 845 51. Miková, E., Varcholová, K., Boldogh, S. & Uhrin, M. Winter diet analysis in *Rhinolophus euryale* (Chiroptera). *Open Life Sciences* **8**, 848–
846 853 (2013).
- 847 52. Arthur, L. & Lemaire, M. *Les Chauves-souris de France Belgique Luxembourg et Suisse*. (Biotope, 2009).
- 848 53. Fitch, H. S. Ecology of the California Ground Squirrel on Grazing Lands. *The American Midland Naturalist* **39**, 513–596 (1948).
- 849 54. Ransome, R. D. The distribution of the Greater horse-shoe bat, *Rhinolophus ferrum-equinum*, during hibernation, in relation to
850 environmental factors. *Journal of Zoology* **154**, 77–112 (1968).
- 851 55. Harmata, W. The length of awakening time from hibernation of three species of bats. *Acta Theriol.* **30**, 321–323 (1985).
- 852 56. Bronson, M. T. *Altitudinal Variation in the Annual Cycle and Life History of the Golden-mantled Ground Squirrel (Spermophilus Lateralis)*.
853 (University of California, Berkeley, 1977).
- 854 57. Bartels, M. A. & Thompson, D. P. *Spermophilus lateralis*. *Mamm Species* 1–8 (1993) doi:10.2307/3504114.
- 855 58. Clark, T. W. Notes on the biology of the thirteen-lined ground squirrel in the Laramie Plains, Wyoming. *The Southwestern Naturalist* **15**,
856 499–502 (1971).
- 857 59. Streubel, D. P. & Fitzgerald, J. P. *Spermophilus tridecemlineatus*. *Mamm Species* 1–5 (1978) doi:10.2307/3504003.
- 858 60. Nikol'skii, A. A. Temperature conditions in burrows of the steppe marmot, *Marmota bobak* Müller (1776), in the hibernation period. *Russian*
859 *journal of ecology* **40**, 529 (2009).

- 860 61. Braun, J. K., Eaton Jr, T. S. & Mares, M. A. *Marmota caligata* (Rodentia: Sciuridae). *Mammalian Species* **43**, 155–171 (2011).
- 861 62. Armitage, K. B. Social and population dynamics of yellow-bellied marmots: results from long-term research. *Annual Review of Ecology and*
862 *Systematics* **22**, 379–407 (1991).
- 863 63. Frase, B. A. & Hoffmann, R. S. *Marmota flaviventris*. *Mamm Species* 1–8 (1980) doi:10.2307/3503965.
- 864 64. Walter, A. The evolution of marmot sociality: II. Costs and benefits of joint hibernation. *Behavioral Ecology and Sociobiology* **27**, 239–246
865 (1990).
- 866 65. Zervanos, S. M., Maher, C. R., Waldvogel, J. A. & Florant, G. L. Latitudinal Differences in the Hibernation Characteristics of Woodchucks
867 (*Marmota monax*). *Physiological and Biochemical Zoology* **83**, 135–141 (2010).
- 868 66. Bryant, A. A. & Page, R. E. Timing and causes of mortality in the endangered Vancouver Island marmot (*Marmota vancouverensis*).
869 *Canadian Journal of Zoology* **83**, 674–682 (2005).
- 870 67. Dobson, F. S. & Davis, D. E. Hibernation and Sociality in the California Ground Squirrel. *Journal of Mammalogy* **67**, 416–421 (1986).
- 871 68. Hayssen, V. Patterns of Body and Tail Length and Body Mass in Sciuridae. *J Mammal* **89**, 852–873 (2008).
- 872 69. Smith, J. E., Long, D. J., Russell, I. D., Newcomb, K. L. & Muñoz, V. D. *Otospermophilus beecheyi* (Rodentia: Sciuridae). *Mamm Species*
873 **48**, 91–108 (2016).
- 874 70. Ortega, J. C. The annual cycles of activity and weight of rock squirrels (*Spermophilus variegatus*) in southeastern Arizona. *American*
875 *Midland Naturalist* 159–171 (1991).
- 876 71. Steiner, A. L. Bedding and Nesting Material Gathering in Rock Squirrels, *Spermophilus* (*Otospermophilus*) *variegatus grammurus* (Say)
877 (*Sciuridae*) in the Chiricahua Mountains of Arizona. *The Southwestern Naturalist* **20**, 363–369 (1975).
- 878 72. Ortega, J. C. Den Site Selection by the Rock Squirrel (*Spermophilus variegatus*) in Southeastern Arizona. *J Mammal* **68**, 792–798 (1987).
- 879 73. Young, P. J. Summer activity patterns of rock squirrels in central Texas. (Texas Tech University, 1979).
- 880 74. Oaks, E. C., Young, P. J., Kirkland, G. L. & Schmidt, D. F. *Spermophilus variegatus*. *Mamm Species* 1–8 (1987) doi:10.2307/3503949.

- 881 75. Murie, J. O. Population Characteristics and Phenology of a Franklin Ground Squirrel (*Spermophilus franklinii*) Colony in Alberta, Canada.
882 *The American Midland Naturalist* **90**, 334–340 (1973).
- 883 76. Ostroff, A. C. & Finck, E. J. *Spermophilus franklinii*. *Mamm Species* 1–5 (2003) doi:10.1644/0.724.1.
- 884 77. Millesi, E., Strijkstra, A. M., Hoffmann, I. E., Dittami, J. P. & Daan, S. Sex and Age Differences in Mass, Morphology, and Annual Cycle in
885 European Ground Squirrels, *Spermophilus citellus*. *J Mammal* **80**, 218–231 (1999).
- 886 78. Luo, J. & Fox, B. J. Life-Table Comparisons between Two Ground Squirrels. *J Mammal* **71**, 364–370 (1990).
- 887 79. Belovezhets, K. I. & Nikol'skii, A. A. Temperature regime in burrows of ground squirrels (Marmotinae) during winter hibernation. *Russ J*
888 *Ecol* **43**, 155–161 (2012).
- 889 80. Broadbooks, H. E. Populations of the Yellow-Pine Chipmunk, *Eutamias amoenus*. *The American Midland Naturalist* **83**, 472–488 (1970).
- 890 81. Broadbooks, H. E. Life History and Ecology of the Chipmunk, *Eutamias amoenus*, in Eastern Washington. 56 (1958).
- 891 82. Sutton, D. A. *Tamias amoenus*. *Mammalian species* 1–8 (1992).
- 892 83. Broadbooks, H. E. Tree nests of chipmunks with comments on associated behavior and ecology. *Journal of Mammalogy* **55**, 630–639 (1974).
- 893 84. Bryant, M. D. Phylogeny of nearctic Sciuridae. *The American Midland Naturalist* **33**, 257–390 (1945).
- 894 85. Kawamichi, M. Nest Structure Dynamics and Seasonal Use of Nests by Siberian Chipmunks (*Eutamias sibiricus*). *J Mammal* **70**, 44–57
895 (1989).
- 896 86. Youlatos, D., Michael, D. E. & Tokalaki, K. Positional behavior of Siberian chipmunks (*Tamias sibiricus*) in captivity. *J Ethol* **26**, 51–60
897 (2008).
- 898 87. Humphries, M. M., Kramer, D. L. & Thomas, D. W. The Role of Energy Availability in Mammalian Hibernation: An Experimental Test in
899 Free-Ranging Eastern Chipmunks. *Physiological and Biochemical Zoology* **76**, 180–186 (2003).
- 900 88. Clarke, M. F. *et al.* Site familiarity affects escape behaviour of the eastern chipmunk, *Tamias striatus*. *Oikos* 533–537 (1993).
- 901 89. Pilon, L. & Baron, G. Distribution spatio-temporelle de l'activité chez *Tamias striatus*. *Mammalia* **54**, 391–396 (1990).

- 902 90. Essner, R. L. Morphology, locomotor behaviour and microhabitat use in North American squirrels. *J Zoology* **272**, 101–109 (2007).
- 903 91. Kenagy, G. J. & Barnes, B. M. Seasonal Reproductive Patterns in Four Coexisting Rodent Species from the Cascade Mountains, Washington.
904 *J Mammal* **69**, 274–292 (1988).
- 905 92. Sutton, D. A. *Tamias townsendii*. *Mamm Species* 1–6 (1993) doi:10.2307/3504166.
- 906 93. Carey, A. B. *The biology of arboreal rodents in Douglas-fir forests*. vol. 276 (US Department of Agriculture, Forest Service, Pacific
907 Northwest Research Station, 1992).
- 908 94. Wilk, R. J., Harrington, T. B., Gitzen, R. A. & Maguire, C. C. Forest-Floor Disturbance Reduces Chipmunk (*Tamias* spp.) Abundance Two
909 Years after Variable-Retention Harvest of Pacific Northwestern Forests. *nwsc* **89**, 75–92 (2015).
- 910 95. Knopf, F. L. & Balph, D. F. Annual Periodicity of Uinta Ground Squirrels. *The Southwestern Naturalist* **22**, 213–224 (1977).
- 911 96. Slade, N. A. & Balph, D. F. Population Ecology of Uinta Ground Squirrels. *Ecology* **55**, 989–1003 (1974).
- 912 97. Eshelman, B. D. & Sonnemann, C. S. *Spermophilus armatus*. *Mamm Species* 1–6 (2000) doi:10.2307/0.637.1.
- 913 98. Loehr, K. A. & Risser, A. C. Daily and Seasonal Activity Patterns of the Belding Ground Squirrel in the Sierra Nevada. *Journal of*
914 *Mammalogy* **58**, 445–448 (1977).
- 915 99. Zammuto, R. M. & Sherman, P. W. A comparison of time-specific and cohort-specific life tables for Belding's ground squirrels,
916 *Spermophilus beldingi*. *Can. J. Zool.* **64**, 602–605 (1986).
- 917 100. Jenkins, S. H. & Eshelman, B. D. *Spermophilus beldingi*. *Mamm Species* 1–8 (1984) doi:10.2307/3503911.
- 918 101. Sherman, P. W. & Runge, M. C. Demography of a Population Collapse: The Northern Idaho Ground Squirrel (*spermophilus Brunneus*
919 *Brunneus*). *Ecology* **83**, 2816–2831 (2002).
- 920 102. Yensen, E. & Sherman, P. W. *Spermophilus brunneus*. *Mamm Species* 1–5 (1997) doi:10.2307/3504405.
- 921 103. Dobson, F. S., Badry, M. J. & Geddes, C. Seasonal activity and body mass of Columbian ground squirrels. *Can. J. Zool.* **70**, 1364–1368
922 (1992).

- 923 104. Neuhaus, P., Broussard, D. R., Murie, J. O. & Dobson, F. S. Age of Primiparity and Implications of Early Reproduction on Life History in
924 Female Columbian Ground Squirrels. *Journal of Animal Ecology* **73**, 36–43 (2004).
- 925 105. Elliott, C. L. & Flinders, J. T. *Spermophilus columbianus*. *Mamm Species* 1–9 (1991) doi:10.2307/3504178.
- 926 106. Sheriff, M. J. *et al.* Phenological variation in annual timing of hibernation and breeding in nearby populations of Arctic ground squirrels.
927 *Proceedings of the Royal Society B: Biological Sciences* **278**, 2369–2375 (2011).
- 928 107. Wilbur, S. M. Demographics and telomere dynamics of hibernating Arctic ground squirrels (*Urocitellus parryii*). (2019).
- 929 108. McLean, B. S. *Urocitellus parryii* (Rodentia: Sciuridae). *Mamm Species* **50**, 84–99 (2018).
- 930 109. Michener, G. R. The Circannual Cycle of Richardson’s Ground Squirrels in Southern Alberta. *J Mammal* **60**, 760–768 (1979).
- 931 110. Michener, G. R. Reproductive effort during gestation and lactation by Richardson’s ground squirrels. *Oecologia* **78**, 77–86 (1989).
- 932 111. Michener, G. R. & Koepl, J. W. *Spermophilus richardsonii*. *Mammalian Species* 1–8 (1985).
- 933 112. Ernest, K. A. & Mares, M. A. *Spermophilus tereticaudus*. *Mammalian Species* 1–9 (1987).
- 934 113. Best, T. L. *Spermophilus mohavensis*. *Mammalian Species* 1–7 (1995).
- 935 114. Munroe, K. E. The Socioecology, Mating System and Behavior of Round-Tailed Ground Squirrels (*Xerospermophilus tereticaudus*). (2011).
- 936 115. Nicol, S. C. & Morrow, G. E. Sex and Seasonality: Reproduction in the Echidna (*Tachyglossus aculeatus*). in *Living in a Seasonal World:
937 Thermoregulatory and Metabolic Adaptations* (eds. Ruf, T., Bieber, C., Arnold, W. & Millesi, E.) 143–153 (Springer, 2012). doi:10.1007/978-3-
938 642-28678-0_13.
- 939 116. Levesque, D. L., Lovasoa, O. M. A., Rakotoharimalala, S. N. & Lovegrove, B. G. High mortality and annual fecundity in a free-ranging basal
940 placental mammal, *Setifer setosus* (Tenrecidae: Afrosoricida). *Journal of Zoology* **291**, 205–212 (2013).
- 941 117. Stankowich, T. & Stensrud, C. Small but spiny: the evolution of antipredator defenses in Madagascar tenrecs. *J Mammal* **100**, 13–20 (2019).
- 942 118. Levesque, D. L., Rakotondravony, D. & Lovegrove, B. G. Home range and shelter site selection in the greater hedgehog tenrec in the dry
943 deciduous forest of Western Madagascar. *Journal of Zoology* **287**, 161–168 (2012).

- 944 119. Lovegrove, B. G., Lobban, K. D. & Levesque, D. L. Mammal survival at the Cretaceous–Palaeogene boundary: metabolic homeostasis in
945 prolonged tropical hibernation in tenrecs. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20141304 (2014).
- 946 120. Nowak, R. M. *Walker's mammals of the world: monotremes, marsupials, afrotherians, xenarthrans, and sundatherians*. (JHU Press, 2018).
- 947 121. Lohuis, T. D., Harlow, H. J., Beck, T. D. I. & Iaizzo, P. A. Hibernating Bears Conserve Muscle Strength and Maintain Fatigue Resistance.
948 *Physiological and Biochemical Zoology* **80**, 257–269 (2007).
- 949 122. Manchi, S. & Swenson, J. E. Denning behaviour of Scandinavian brown bears *Ursus arctos*. *wbio* **11**, 123–132 (2005).
- 950 123. Reid, D., Jiand, M., Teng, Q., Qin, Z. & Hu, J. Ecology of the asiatic black bear (*Ursus thibetanus*) in Sichuan, China. *Mammalia* **55**, 221–
951 238 (1991).
- 952 124. Seryodkin, I. V. *et al.* Denning ecology of brown bears and Asiatic black bears in the Russian Far East. *Ursus* 153–161 (2003).
- 953 125. Reid, D., Jiang, M., Teng, Q., Qin, Z. & Hu, J. Ecology of the asiatic black bear (*Ursus thibetanus*) in Sichuan, China. *Mammalia* **55**, 221–
954 238 (1991).
- 955 126. Baranauskas, K. Hibernation of Barbastelle (*Barbastella Barbastellas*) in Šeškinė Bunkers in Vilnius (Lithuania). A Possible Bat Population
956 Response to Climate change. *Acta Zoologica Lituanica* **11**, 15–19 (2001).
- 957 127. Johnson, J. S., Lacki, M. J., Thomas, S. C. & Grider, J. F. Frequent arousals from winter torpor in Rafinesque's big-eared bat (*Corynorhinus*
958 *rafinesquii*). *PLoS One* **7**, (2012).
- 959 128. Jones, C. *Plecotus rafinesquii*. *Mamm Species* 1–4 (1977) doi:10.2307/3503868.
- 960 129. Beer, J. R. & Richards, A. G. Hibernation of the big brown bat. *Journal of Mammalogy* **37**, 31–41 (1956).
- 961 130. Rydell, J. *Eptesicus nilssonii*. *Mammalian species* 1–7 (1993).
- 962 131. Robinson, M. F. & Stebbings, R. E. Activity of the serotine bat, *Eptesicus serotinus*. *England. Myotis* **35**, 5–16 (1997).
- 963 132. Weller, T. J. *et al.* First direct evidence of long-distance seasonal movements and hibernation in a migratory bat. *Scientific reports* **6**, 1–7
964 (2016).
- 965 133. Jones, C. & Manning, R. W. *Myotis austroriparius*. *Mamm Species* 1–3 (1989) doi:10.2307/3504306.

- 966 134. Rice, D. W. Life history and ecology of *Myotis austroriparius* in Florida. *Journal of Mammalogy* **38**, 15–32 (1957).
- 967 135. Podlutzky, A. J., Khritankov, A. M., Ovodov, N. D. & Austad, S. N. A new field record for bat longevity. *The Journals of Gerontology Series*
968 *A: Biological Sciences and Medical Sciences* **60**, 1366–1368 (2005).
- 969 136. Limpens, H., Lina, P. H. C. & Hutson, A. M. Action plan for the conservation of the pond bat (*Myotis dasycneme*) in Europe. *Council of*
970 *Europe, Strasbourg* (1999).
- 971 137. Baranauskas, K. The first data about the hibernation of Daubenton's bat (*Myotis daubentonii*) in the Paneriai tunnel (Vilnius, Lithuania). *Acta*
972 *Zoologica Lituanica* **13**, 379–384 (2003).
- 973 138. Decher, J. & Choate, J. R. *Myotis grisescens*. *Mammalian Species* 1–7 (1995).
- 974 139. Caire, W., LaVal, R. K., LaVal, M. L. & Clawson, R. Notes on the ecology of *Myotis keenii* (Chiroptera, Vespertilionidae) in eastern
975 Missouri. *American Midland Naturalist* 404–407 (1979).
- 976 140. Norquay, K. J. O. & Willis, C. K. R. Hibernation phenology of *Myotis lucifugus*. *Journal of Zoology* **294**, 85–92 (2014).
- 977 141. Zahn, A., Rodrigues, L., Rainho, A. & Palmeirim, J. M. Critical times of the year for *Myotis myotis*, a temperate zone bat: roles of climate
978 and food resources. *Acta Chiropterologica* **9**, 115–125 (2007).
- 979 142. Kaupas, L. Roosting Behaviour and Thermoregulation of the Northern Long-Eared Bat (*Myotis septentrionalis*) Near the Northern Extent of
980 its Range. (Graduate Studies, 2016).
- 981 143. Wilkinson, G. S. & South, J. M. Life history, ecology and longevity in bats. *Aging Cell* **1**, 124–131 (2002).
- 982 144. Kurta, A. *Mammals of the Great Lakes Region*. (The University of Michigan, 1995).
- 983 145. Caceres, M. C. & Barclay, R. M. R. *Myotis septentrionalis*. *Mamm Species* 1–4 (2000) doi:10.2307/0.634.1.
- 984 146. Clawson, R. L., LaVal, R. K., LaVal, M. L. & Caire, W. Clustering behavior of hibernating *Myotis sodalis* in Missouri. *Journal of*
985 *Mammalogy* **61**, 245–253 (1980).
- 986 147. Caire, W. & Loucks, L. S. Loss in mass by hibernating Cave Myotis, *Myotis velifer* (Chiroptera: Vespertilionidae) in western Oklahoma. *The*
987 *Southwestern Naturalist* **55**, 323–330 (2010).

- 988 148. J.w, S. & P.f, V. H. Seasonal Habits of the Noctule Bat (*Nyctalus Noctula*). *Archives Néerlandaises de Zoologie* **16**, 423–439 (1964).
- 989 149. Dalhoumi, R., Morellet, N., Aissa, P. & Aulagnier, S. Seasonal activity pattern and habitat use by the Kuhl's pipistrelle (*Pipistrellus kuhlii*) in
990 an arid environment. *European journal of wildlife research* **64**, 36 (2018).
- 991 150. Racey, P. A. Ageing and assessment of reproductive status of pipistrelle bats, *Pipistrellus pipistrellus*. *Journal of Zoology* **173**, 264–271
992 (1974).
- 993 151. Damm, J. P. & Geluso, K. Use of a mine by eastern pipistrelles (*Perimyotis subflavus*) in east central Nebraska. *Western North American*
994 *Naturalist* **68**, 382–389 (2008).
- 995 152. Stebbings, R. E. A Comparative Study of *Plecotus Auritus* and *P. Austriacus* (Chiroptera, Vespertilionidae) Inhabiting One Roost. *Bijdragen*
996 *tot de Dierkunde* **40**, 91–94 (1970).
- 997 153. Herrero, S. Aspects of evolution and adaptation in American black bears (*Ursus americanus* Pallas) and brown and grizzly bears (*U. arctos*
998 Linne.) of North America. *Bears: Their biology and management* 221–231 (1972).

999

1000

1001

1002

1003

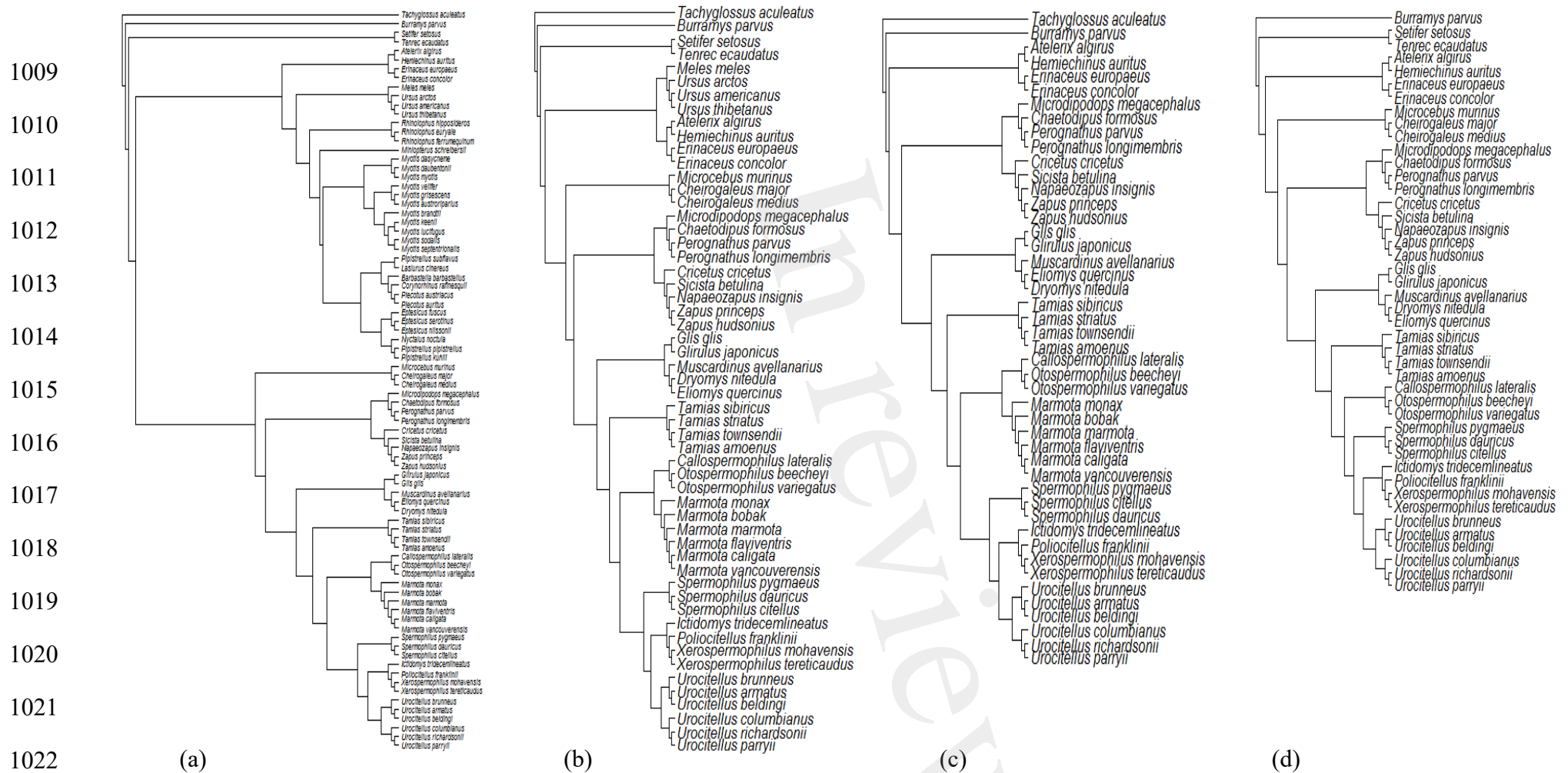
1004

1005

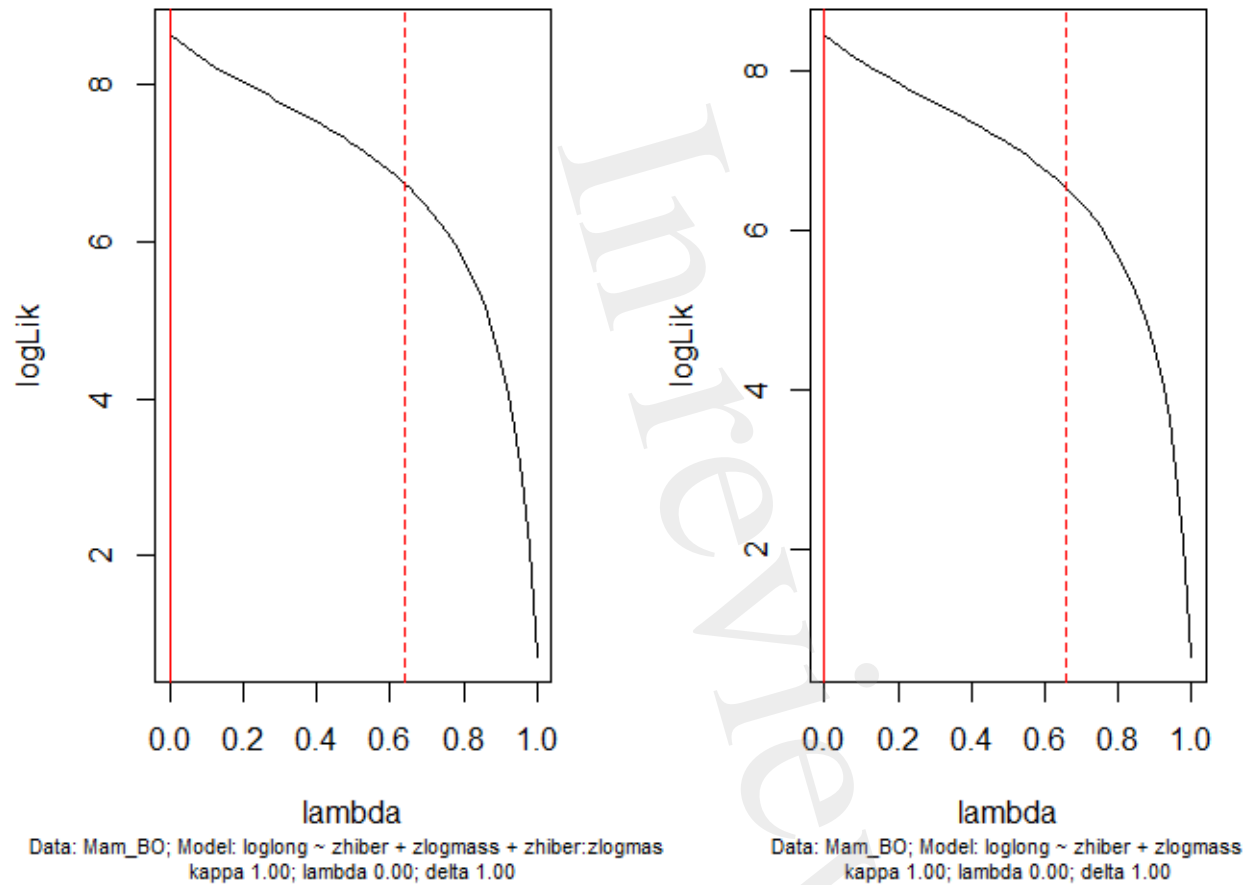
1006

1007

1008



1024 Figure S1. Consensus phylogenetic trees for the species under study: (a) all hibernators data set (N = 82), (b) the data set without bats (N = 55), (c) the
 1025 data set of deep hibernators without bats (N = 46) and (d) the data set of small hibernators (<1.5 kg) without bats (N = 44). Each consensus tree was
 1026 built from 100 trees obtained from <http://vertlife.org/phylosubsets/>. Branch lengths were calculated using Grafen's computations with the 'ape' package
 1027 in R (see Methods).



1028

1029 Figure S2: Likelihood profile of λ s for bat models only ($N = 27$): (a) including the effects of hibernation season duration (standardized), body mass
 1030 (standardized and log transformed) and interaction hibernation duration x body mass, (b) without interaction. logLik represent the likelihood value
 1031 log-transformed. Lambda (λ) correspond to the relative effect of the phylogenetic tree on the linear model, ranging between 0 (covariation among
 1032 species measurements is independent of co-ancestry) and 1 (covariance entirely explained by co-ancestry). Location of the maximum likelihood
 1033 estimate of λ is symbolised by a red line, upper 95% CI is symbolized by a dashed red line. Note that the lower 95% CI can not be estimated.

1034

		Model terms	λ_{ML}	
			AIC	R^2 / R^2_{adj}
Phylogenetic correction (PGLS)	Model 1: All hibernators (82 species)	zhiber+zlogmass+zhiber:zlogmass+C_W+bats+arboreality	-50.51046	0.2653/ 0.2065
		zhiber+zlogmass+C_W+bats+arboreality	-52.49145	0.2637/ 0.2152
		zhiber+zlogmass+bats+arboreality	-52.01818	0.2242/0.1839
	Model 2: Hibernators without bats (55 species)	zhiber+zlogmass+zhiber:zlogmass+C_W+arboreality	-42.84827	0.4048/0.3441
		zhiber+zlogmass+C_W+arboreality	-44.84158	0.4038/0.3561
		zhiber+zlogmass+arboreality	-44.92069	0.3744/0.3376
	Model 3: Deep hibernators without bats (46 species)	zhiber+zlogmass+zhiber:zlogmass+C_W+arboreality	-37.18019	0.2105/0.1118
		zhiber+zlogmass+C_W+arboreality	-39.17963	0.2104/0.1334
		zhiber+zlogmass+arboreality	-38.92486	0.1718/0.1126
		zhiber+zlogmass+	-40.34324	0.1592/0.1201
	Model 4: Small hibernators (<1,5 kg) without bats (44 species)	zhiber+zlogmass+zhiber:zlogmass+C_W+arboreality	-48.57117	0.3206/0.2312
		zhiber+zlogmass+C_W+arboreality	-49.04655	0.3038/0.2324
zhiber+zlogmass+arboreality		-48.3023	0.2662/0.2112	
No phylogenetic correction (linear model)	Model 5: Bats only (27 species)	zhiber+zlogmass+zhiber:zlogmass	-7.308115	0.193/0.0877
		zhiber+zlogmass	-8.912492	0.1811/0.1128

1035

1036 Table S3: Model selection for the effects of hibernation season duration (zhiber), body mass (zlogmass), the interaction zhiber x zlogmass, bats and
1037 arboreality lifestyle and the effect of captivity (C_W; captive vs. wild) on longevity in hibernating mammals.

In review