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Integrating mortality risks and the adaptiveness of hibernation

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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

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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

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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

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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

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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

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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

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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

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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)

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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

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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).

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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).

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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

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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,

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386 2004). Thus, food availability and ambient temperature alone may not be sufficient to explain the
387 phenology of immergence.

388 Other evidence suggests that hibernation is not initiated solely in response to deficiencies in
389 energy, water, or poor food quality. Many observations suggest that early immergence (before
390 energetically stressful periods start) occurs when the benefits of reproduction are low. For instance, in
391 years of low beech seed abundance, the edible dormouse (*Glis glis*) skips reproduction, quickly
392 accumulates fat reserves, and is able to hibernate for up to 11 months (Hoelzl et al., 2015). This occurs
393 even if food in the environment is sufficient to allow the edible dormouse to remain active but not to
394 reproduce. Similarly, Eastern chipmunks skip reproduction and cease foraging for almost a full year
395 when food availability is particularly low (Munro et al., 2008). It seems that at that time, chipmunks
396 rely on large amounts of food hoarded during the preceding year; but there is no evidence of torpor
397 expression. This kind of behaviour is also observed in several hibernating ground squirrel species.
398 Females that fail to reproduce may immerge up to several weeks before the others (Bintz, 1988;
399 Choromanski-Norris et al., 1986; Michener, 1978; Neuhaus, 2000). An experiment in semi-natural
400 conditions shows that female European ground squirrels (*Spermophilus citellus*) that were separated
401 from males (and thus did not breed) entered into hibernation 4 to 6 weeks before females that were not
402 separated (Millesi et al., 2008). These results support the view that hibernation phenology is influenced
403 by a trade-off between reproduction and survival, where hibernation seems to provide benefits other
404 than surviving periods of energetic stress. This trade-off may also explain differences (up to 1 month)
405 in the timing of immergence and emergence between gender and age observed in rodents (Siutz et al.,
406 2016; Sheriff et al., 2011; Kawamichi, 1989 ; Kart Gür and Gür, 2015; Snyder et al., 1961; Holekamp
407 and Nunes, 1989) and bats (Decher and Choate, 1995; Norquay and Willis, 2014; Stebbings, 1970;
408 Thomson, 1982).

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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.

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In review

Time dimension of allocation trade-offs in hibernators

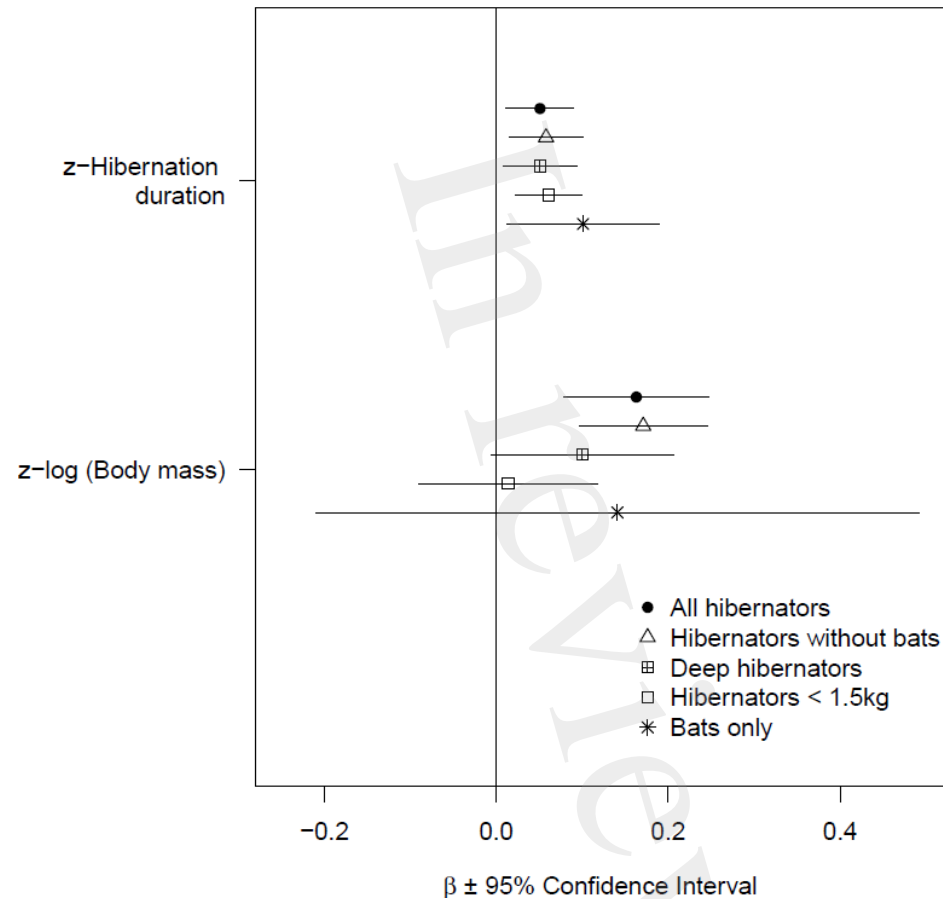
Model	1	2	3	4	5
Model type	PGLS	PGLS	PGLS	PGLS	Linear model
Hibernators > 1.5 kg	x	x			
Hibernators < 1.5 kg	x	x		x	
Deep hibernators	x	x	x		
Bats	x				x
Sample size	82	55	46	44	27
Arboreal and semi-arboreal species	16	16	11	15	0
Hibernation season duration range (day)	105-296	105-296	105-296	105-296	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

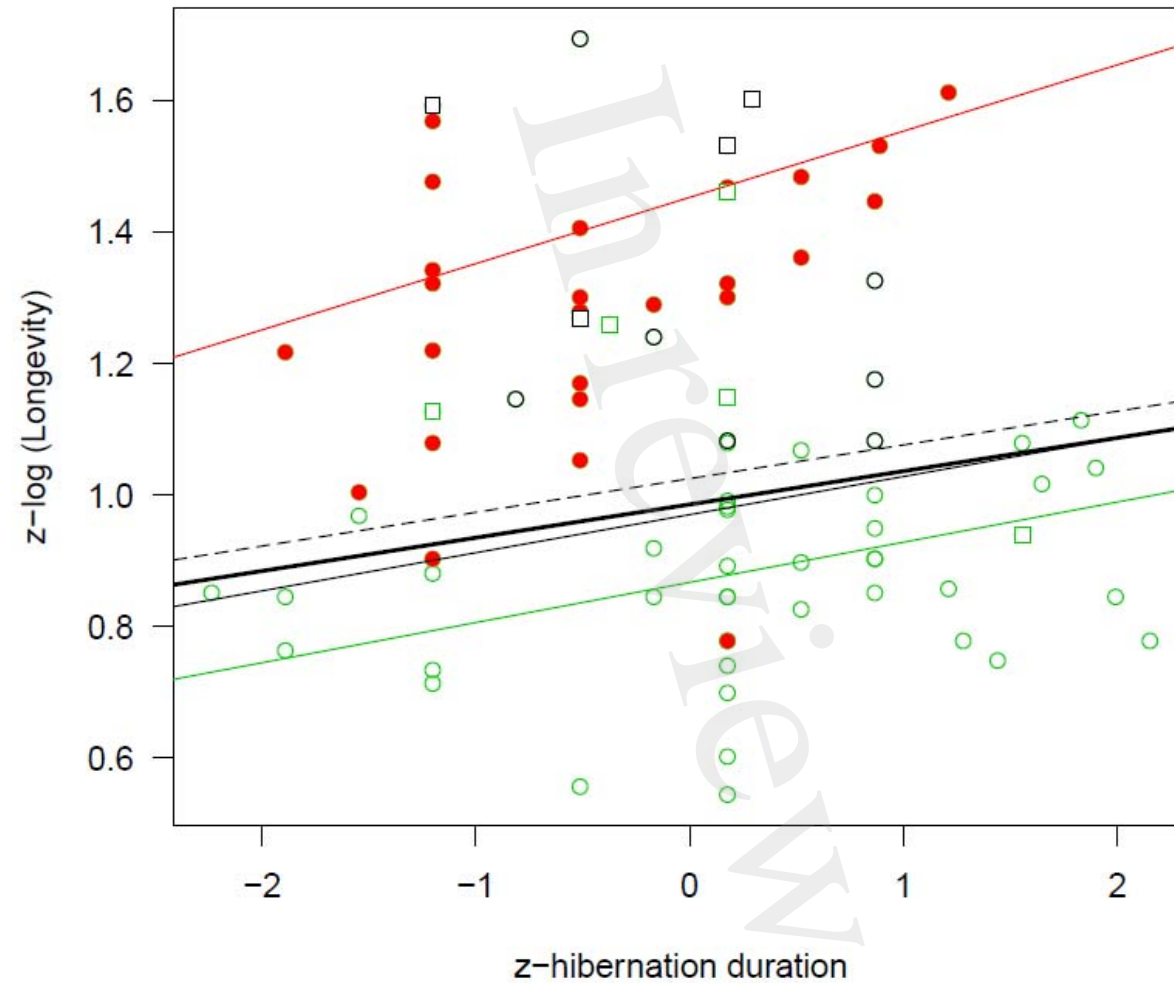
			λ_{ML}				$\lambda = 0$		
			λ_{ML}	$\beta \pm SE$	t	P	$\beta \pm SE$	t	P
Phylogenetic correction (PGLS)	Model 1: All hibernators (82 species)	Intercept	$\lambda_{ML} = 0.736$ $CI_{95} = [NA-0.924]$	0.986 ± 0.111	8.847	< 0.001***	0.834 ± 0.032	25.778	< 0.001***
		z-Hibernation duration		0.051 ± 0.020	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, $N = 55$, $p=0.011$),
 711 deep 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>Vespertilio 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

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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
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- 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.

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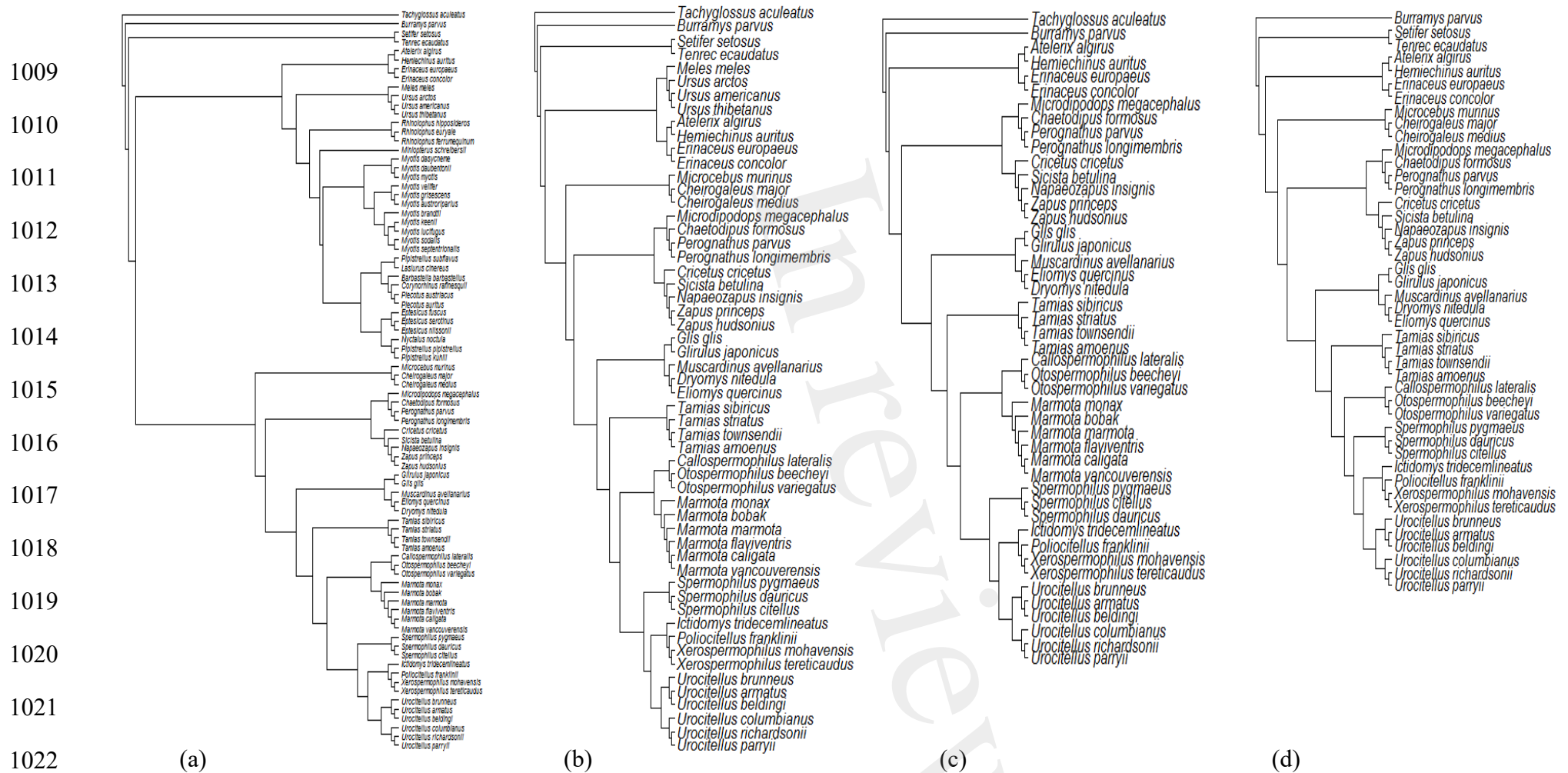
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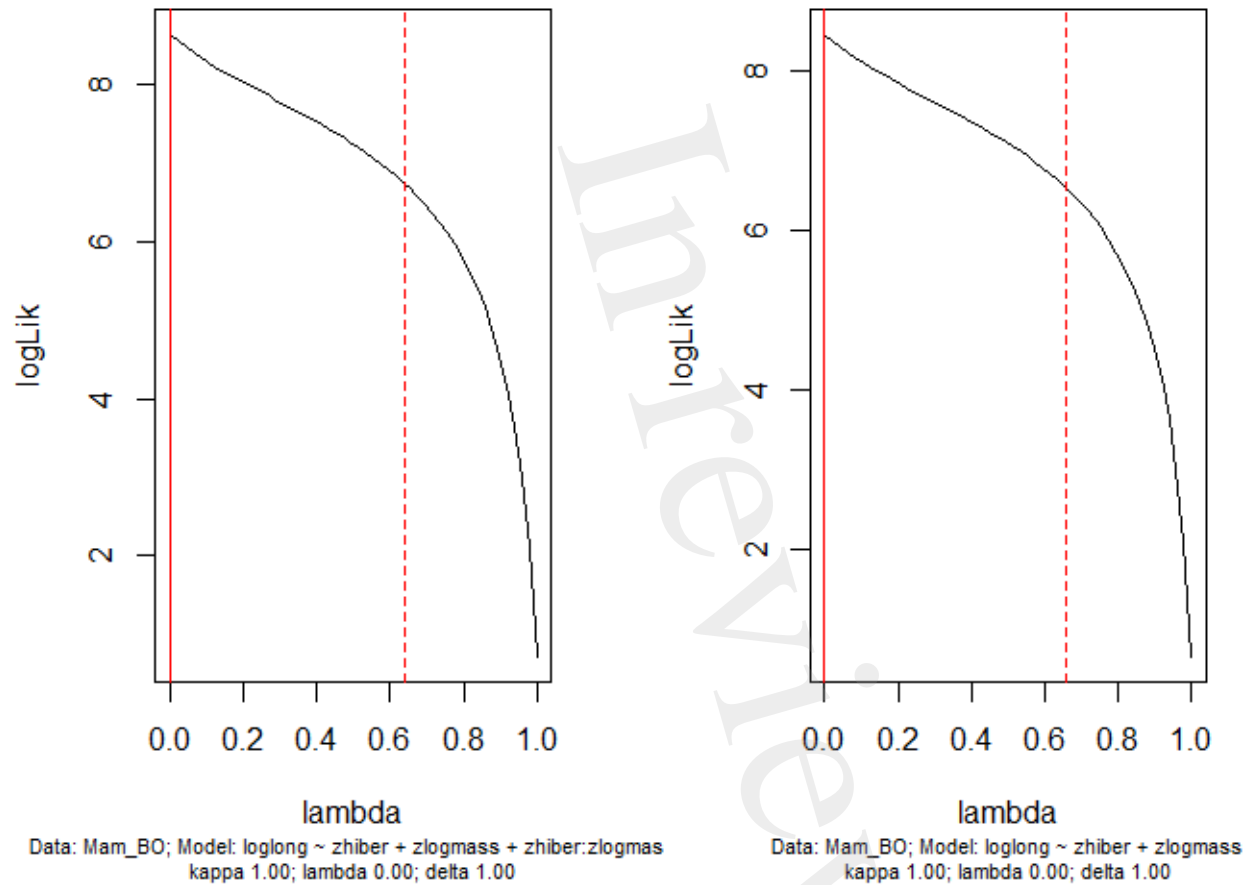
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1024 Figure S1. Consensus phylogenetic trees for the species under study: (a) all hibernators data set (N = 82), (b) the data set without bats (N = 55), (c) the
 1025 data set of deep hibernators without bats (N = 46) and (d) the data set of small 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